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WILLIAM BATESON

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PREFACE

WITH certain exceptions the present volume contains Bateson's papers treating of heredity. The exceptions comprise those papers of more general interest which have already been reprinted in *William Bateson—Naturalist*[1], and also the more technical portions of the series of *Reports to the Evolution Committee of the Royal Society*, 1902–8, which can still be purchased from the Royal Society.

The more important of Bateson's reviews of scientific works relating to heredity will be found at the end of the volume.

I would take this opportunity of expressing my thanks to Mrs Bateson and to Mr Gregory Bateson for much help in the preparation of the Bibliography.

Thanks are due to the following Societies for permission to reprint papers which have appeared in their journals: the Cambridge Philosophical Society, the Royal Society, the Royal Horticultural Society, and the Zoological Society of London; also to the Editors and Publishers of *The British Medical Journal*, *The Eugenics Review*, *The Journal of Genetics*, *Nature*, *Science* (U.S.A.), and *Studia Mendeliana*.

[1] Cambridge University Press, 1928.

R. C. PUNNETT

August 1928

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EXPERIMENTS IN PLANT HYBRIDISATION

[*Journal of the Royal Horticultural Society*, XXVI, 1901]

The original paper, of which the following pages are a translation, was published by Gregor Mendel in the year 1865 in the *Abhandlungen des naturforschenden Vereines in Brünn*, Bd. IV. That periodical is little known, and probably there are not half a dozen copies in the libraries of this country. It will consequently be a matter for satisfaction that the Royal Horticultural Society has undertaken to publish a translation of this extraordinarily valuable contribution to biological science.

The conclusion which stands out as the chief result of Mendel's admirable experiments is of course the proof that in respect of certain pairs of differentiating characters the germ cells of a hybrid, or cross-bred, are *pure*, being carriers and transmitters of either the one character or the other, not both. That he succeeded in demonstrating this law for the simple cases with which he worked it is scarcely possible to doubt.

In so far as Mendel's law applies, therefore, the conclusion is forced upon us that a living organism is a complex of characters, of which some, at least, are dissociable and are capable of being replaced by others. We thus reach the conception of *unit-characters*, which may be rearranged in the formation of the reproductive cells. It is hardly too much to say that the experiments which led to this advance in knowledge are worthy to rank with those that laid the foundation of the Atomic laws of Chemistry.

To what extent Mendel's conclusions will be found to apply to other characters, and to other plants and animals, further experiment alone can show. Though little has yet been done, we already know a considerable group of cases in which the law holds, but we also have tolerably clear evidence that many phenomena of cross-breeding point to the coexistence of other laws of a much higher order of complexity. When the paper before us was written Mendel apparently inclined to the view that, with modifications, his law might be found to include all the phenomena of hybridisation, but in a brief subsequent paper on hybrids of the genus *Hieracium*[1] he clearly recognised the existence of unconformable cases.

Nevertheless, however much it may be found possible to limit or to

[1] *Verh. naturf. Ver. Brünn*, VIII, 1869, p. 26.

extend the principle discovered by Mendel, there can be no doubt that we have in his work not only a model for future experiments of the same kind, but also a solid foundation from which the problem of Heredity may be attacked in the future.

It may seem surprising that a work of such importance should so long have failed to find recognition and to become current in the world of science. It is true that the journal in which it appeared is scarce, but this circumstance has seldom long delayed general recognition. The cause is unquestionably to be found in the neglect of the experimental study of the problem of Species which supervened on the general acceptance of the Darwinian doctrines. The problem of Species, as Gärtner, Kölreuter, Naudin, Mendel, and the other hybridists of the first half of the nineteenth century conceived it, attracted thenceforth no workers. The question, it was imagined, had been answered and the debate ended. No one felt any interest in the matter. A host of other lines of work were suddenly opened up, and in 1865 the more vigorous investigators naturally found those new methods of research more attractive than the tedious observations of the hybridisers, whose inquiries were supposed to have led to no definite result. But if we are to make progress with the study of Heredity, and to proceed further with the problem "What *is* a Species?" as distinct from the other problem "How do Species survive?" we must go back and take up the thread of the inquiry exactly where Mendel dropped it.

As was stated in a lecture to the Royal Horticultural Society in 1900 it is to de Vries, Correns, and Tschermak that we owe the simultaneous rediscovery, confirmation and extension of Mendel's work. References[1] are there given to the chief recent publications relating to the subject, of which the number is rapidly increasing.

The whole paper abounds with matters for comment and criticism, which could only be profitable if undertaken at some length. There are also many deductions and lines of inquiry to which Mendel's facts point, which we in a fuller knowledge of physiology can perceive. It may, however, be doubted whether in his own day his conclusions could have been extended.

As some biographical particulars respecting this remarkable investigator will be welcome, I subjoin the following brief notice, which was published by Correns[2] on the authority of Dr von Schanz:

[1] *Journ. Roy. Hort. Soc.* xxv, 1900, p. 54.
[2] *Bot. Zeitg.* LVIII, 1900, No. 15, p. 229.

Gregor Johann Mendel was born on July 22, 1822, at Heinzendorf bei Odrau, in Austrian Silesia. He was the son of well-to-do peasants. In 1843 he entered as a novice the "Königinkloster," an Augustinian foundation in Altbrünn. In 1847 he was ordained priest. From 1851 to 1853 he studied physics and natural science at Vienna. Thence he returned to his cloister and became a teacher in the Realschule at Brünn. Subsequently he was made Abbot, and died January 6, 1884. The experiments described in his papers were carried out in the garden of his Convent.

Besides the two papers on hybridisation, dealing respectively with *Pisum* and *Hieracium*, Mendel contributed to the Brünn journal observations of a meteorological character, but, so far as I am aware, no others relating to natural history.

THE PROBLEMS OF HEREDITY AND THEIR SOLUTION[1]

[*Mendel's Principles of Heredity*, 1902, pp. 1–35]

An exact determination of the laws of heredity will probably work more change in man's outlook on the world, and in his power over nature, than any other advance in natural knowledge that can be clearly foreseen.

There is no doubt whatever that these laws can be determined. In comparison with the labour that has been needed for other great discoveries we may even expect that the necessary effort will be small. It is rather remarkable that while in other branches of physiology such great progress has of late been made, our knowledge of the phenomena of heredity has increased but little; though that these phenomena constitute the basis of all evolutionary science and the very central problem of natural history is admitted by all. Nor is this due to the special difficulty of such inquiries so much as to general neglect of the subject.

It is in the hope of inducing others to follow these lines of investigation that I take the problems of heredity as the subject of this lecture to the Royal Horticultural Society.

No one has better opportunities of pursuing such work than horticulturists and stock breeders. They are daily witnesses of the phenomena of heredity. Their success also depends largely on a knowledge of its laws, and obviously every increase in that knowledge is of direct and special importance to them.

The want of systematic study of heredity is due chiefly to misapprehension. It is supposed that such work requires a lifetime. But though for adequate study of the complex phenomena of inheritance long periods of time must be necessary, yet in our present state of deep ignorance almost of the outline of the facts, observations carefully planned and faithfully carried out for even a few years may produce results of great value. In fact, by far the most appreciable

[1] The first half of this paper is reprinted with additions and modifications from the *Journal of the Royal Horticultural Society*, xxv, 1900, pts. 1 and 2. Written almost immediately after the rediscovery of Mendel, it will be seen to be already in some measure out of date, but it may thus serve to show the relation of the new conceptions to the old.

and definite additions to our knowledge of these matters have been thus obtained.

There is besides some misapprehension as to the kind of knowledge which is especially wanted at this time, and as to the modes by which we may expect to obtain it. The present paper is written in the hope that it may in some degree help to clear the ground of these difficulties by a preliminary consideration of the question: How far have we got towards an exact knowledge of heredity, and how can we get further?

Now this is pre-eminently a subject in which we must distinguish what we *can* do from what we want to do. We *want* to know the whole truth of the matter; we want to know the physical basis, the inward and essential nature, "the causes," as they are sometimes called, of heredity: but we want also to know the laws which the outward and visible phenomena obey.

Let us recognise from the outset that as to the essential nature of these phenomena we still know absolutely nothing. We have no glimmering of an idea as to what constitutes the essential process by which the likeness of the parent is transmitted to the offspring. We can study the processes of fertilisation and development in the finest detail which the microscope manifests to us, and we may fairly say that we have now a considerable grasp of the visible phenomena; but of the nature of the physical basis of heredity we have no conception at all. No one has yet any suggestion, working hypothesis, or mental picture that has thus far helped in the slightest degree to penetrate beyond what we see. The process is as utterly mysterious to us as a flash of lightning is to a savage. We do not know what is the essential agent in the transmission of parental characters, not even whether it is a material agent or not. Not only is our ignorance complete, but no one has the remotest idea how to set to work on that part of the problem. We are in the state in which the students of physical science were, in the period when it was open to anyone to believe that heat was a material substance or not, as he chose.

But apart from any conception of the essential modes of transmission of characters, we *can* study the outward facts of the transmission. Here, if our knowledge is still very vague, we are at least beginning to see how we ought to go to work. Formerly naturalists were content with the collection of numbers of isolated instances of transmission—more especially, striking and peculiar cases—the sudden appearance of highly prepotent forms, and the like. We are now passing out of that stage. It is not that the interest of particular

cases has in any way diminished—for such records will always have their value—but it has become likely that general expressions will be found capable of sufficiently wide application to be justly called "laws" of heredity. That this is so was till recently due almost entirely to the work of Mr F. Galton, to whom we are indebted for the first systematic attempt to enuntiate such a law.

All laws of heredity so far propounded are of a statistical character and have been obtained by statistical methods. If we consider for a moment what is actually meant by a "law of heredity" we shall see at once why these investigations must follow statistical methods. For a "law" of heredity is simply an attempt to declare the course of heredity under given conditions. But if we attempt to predicate the course of heredity we have to deal with conditions and groups of causes wholly unknown to us, whose presence we cannot recognise, and whose magnitude we cannot estimate in any particular case. The course of heredity in particular cases therefore cannot be foreseen.

Of the many factors which determine the degree to which a given character shall be present in a given individual only one is usually known to us, namely, the degree to which that character is present in the parents. It is common knowledge that there is not that close correspondence between parent and offspring which would result were this factor the only one operating; but that, on the contrary, the resemblance between the two is only an uncertain one.

In dealing with phenomena of this class the study of single instances reveals no regularity. It is only by collection of facts in great numbers, and by statistical treatment of the mass, that any order or law can be perceived. In the case of a chemical reaction, for instance, by suitable means the conditions can be accurately reproduced, so that in every individual case we can predict with certainty that the same result will occur. But with heredity it is somewhat as it is in the case of the rainfall. No one can say how much rain will fall to-morrow in a given place, but we can predict with moderate accuracy how much will fall next year, and for a period of years a prediction can be made which accords very closely with the truth.

Similar predictions can from statistical data be made as to the duration of life and a great variety of events, the conditioning causes of which are very imperfectly understood. It is predictions of this kind that the study of heredity is beginning to make possible, and in that sense laws of heredity can be perceived.

We are as far as ever from knowing *why* some characters are trans-

mitted, while others are not; nor can anyone yet foretell which individual parent will transmit characters to the offspring, and which will not; nevertheless the progress made is distinct.

As yet investigations of this kind have been made in only a few instances, the most notable being those of Galton on human stature, and on the transmission of colours in Basset hounds. In each of these cases he has shown that the expectation of inheritance is such that a simple arithmetical rule is approximately followed. The rule thus arrived at is that of the whole heritage of the offspring the two parents together on an average contribute one-half, the four grandparents one-quarter, the eight great-grandparents one-eighth, and so on, the remainder being contributed by the remoter ancestors.

Such a law is obviously of practical importance. In any case to which it applies we ought thus to be able to predict the degree with which the purity of a strain may be increased by selection in each successive generation.

To take a perhaps impossibly crude example, if a seedling show any particular character which it is desired to fix, on the assumption that successive self-fertilisations are possible, according to Galton's law the expectation of purity should be in the first generation of self-fertilisation 1 in 2, in the second generation 3 in 4, in the third 7 in 8, and so on[1].

But already many cases are known to which the rule in any simple form will not apply. Galton points out that it takes no account of individual prepotencies. There are, besides, numerous cases in which on crossing two varieties the character of one variety almost always appears in each member of the first cross-bred generation. Examples of these will be familiar to those who have experience in such matters. The offspring of the Polled Angus cow and the Shorthorn bull is almost invariably polled or with very small loose "scurs." Seedlings raised by crossing *Atropa belladonna* with the yellow-fruited variety have without exception the blackish-purple fruits of the type. In several hairy species when a cross with a glabrous variety is made, the first cross-bred generation is altogether hairy[2].

Still more numerous are examples in which the characters of one variety very largely, though not exclusively, predominate in the offspring.

[1] See later. Galton gave a simple diagrammatic representation of his law in *Nature*, LVII, 1898, p. 293.

[2] These we now recognise as examples of Mendelian "dominance."

These large classes of exceptions—to go no further—indicate that, as we might in any case expect, the principle is not of universal application, and will need various modifications if it is to be extended to more complex cases of inheritance of varietal characters. No more useful work can be imagined than a systematic determination of the precise "law of heredity" in numbers of particular cases.

Until lately the work which Galton accomplished stood almost alone in this field, but quite recently remarkable additions to our knowledge of these questions have been made. In the year 1900 Professor de Vries published a brief account[1] of experiments which he has for several years been carrying on, giving results of the highest value.

The description is very short, and there are several points as to which more precise information is necessary both as to details of procedure and as to statement of results. Nevertheless it is impossible to doubt that the work as a whole constitutes a marked step forward, and the full publication which is promised will be awaited with great interest.

The work relates to the course of heredity in cases where definite *varieties differing* from each other *in some one definite character are* crossed together. The cases are all examples of discontinuous variation: that is to say, cases in which actual intermediates between the parent forms are not usually produced on crossing[2]. It is shown that the subsequent posterity obtained by self-fertilising these cross-breds or hybrids, or by breeding them with each other, break up into the original parent forms according to fixed numerical rule.

Professor de Vries begins by reference to a remarkable memoir by Gregor Mendel[3], giving the results of his experiments in crossing varieties of *Pisum sativum*. These experiments of Mendel's were carried out on a large scale, his account of them is excellent and complete, and the principles which he was able to deduce from them will certainly play a conspicuous part in all future discussions of evolutionary problems. It is not a little remarkable that Mendel's work should have escaped notice, and been so long forgotten.

For the purposes of his experiments Mendel selected seven pairs of characters as follows:

1. Shape of ripe seed, whether round; or angular and wrinkled.

[1] *Comptes Rendus*, March 26, 1900, and *Ber. Deutsch. Bot. Ges.* XVIII, 1900, p. 38.
[2] This conception of discontinuity is of course pre-Mendelian.
[3] "Versuche üb. Pflanzenhybriden" in the *Verh. naturf. Ver. Brünn*, IV, 1865.

2. Colour of "endosperm" (cotyledons), whether some shade of yellow; or a more or less intense green.

3. Colour of the seed skin, whether various shades of grey and grey-brown; or white.

4. Shape of seed pod, whether simply inflated; or deeply constricted between the seeds.

5. Colour of unripe pod, whether a shade of green; or bright yellow.

6. Nature of inflorescence, whether the flowers are arranged along the axis of the plant; or are terminal and form a kind of umbel.

7. Length of stem, whether about 6 or 7 ft. long, or about $\frac{3}{4}$ to $1\frac{1}{2}$ ft.

Large numbers of crosses were made between Peas differing in respect of *one* of each of these pairs of characters. It was found that in each case the offspring of the cross exhibited the character of one of the parents in almost undiminished intensity, and intermediates which could not be at once referred to one or other of the parental forms were not found.

In the case of each pair of characters there is thus one which in the first cross prevails to the exclusion of the other. This prevailing character Mendel calls the *dominant* character, the other being the *recessive* character[1].

That the existence of such "dominant" and "recessive" characters is a frequent phenomenon in cross-breeding, is well known to all who have attended to these subjects.

By letting the cross-breds fertilise themselves Mendel next raised another generation. In this generation were individuals which showed the dominant character, but also individuals which presented the recessive character. Such a fact also was known in a good many instances. But Mendel discovered that in this generation the numerical proportion of dominants to recessives is on an average of cases approximately constant, being in fact *as three to one*. With very considerable regularity these numbers were approached in the case of each of his pairs of characters.

There are thus in the first generation raised from the cross-breds 75 per cent. dominants and 25 per cent. recessives.

These plants were again self-fertilised, and the offspring of each plant separately sown. It next appeared that the offspring of the

[1] Note that by these novel terms the complications involved by use of the expression "prepotent" are avoided.

recessives *remained pure recessive*, and in subsequent generations never produced the dominant again.

But when the seeds obtained by self-fertilising the dominants were examined and sown it was found that the dominants were not all alike, but consisted of two classes, (1) those which gave rise to pure dominants, and (2) others which gave a mixed offspring, composed partly of recessives, partly of dominants. Here also it was found that the average numerical proportions were constant, those with pure dominant offspring being to those with mixed offspring as one to two. Hence it is seen that the 75 per cent. dominants are not really of similar constitution, but consist of twenty-five which are pure dominants and fifty which are really cross-breds, though, like the cross-breds raised by crossing the two original varieties, they only exhibit the dominant character.

To resume, then, it was found that by self-fertilising the original cross-breds the same proportion was always approached, namely—

25 dominants, 50 cross-breds, 25 recessives, or $1D : 2DR : 1R$.

Like the pure recessives, the pure dominants are thenceforth pure, and only give rise to dominants in all succeeding generations studied.

On the contrary the fifty cross-breds, as stated above, have mixed offspring. But these offspring, again, in their numerical proportions, follow the same law, namely, that there are three dominants to one recessive. The recessives are pure like those of the last generation, but the dominants can, by further self-fertilisation, and examination or cultivation of the seeds produced, be again shown to be made up of pure dominants and cross-breds in the same proportion of one dominant to two cross-breds.

The process of breaking up into the parent forms is thus continued in each successive generation, the same numerical law being followed so far as has yet been observed.

Mendel made further experiments with *Pisum sativum*, crossing pairs of varieties which differed from each other in *two* characters, and the results, though necessarily much more complex, showed that the law exhibited in the simpler case of pairs differing in respect of one character operated here also.

In the case of the union of varieties AB and ab differing in two distinct pairs of characters, A and a, B and b, of which A and B are dominant, a and b recessive, Mendel found that in the first cross-bred generation there was only *one* class of offspring, really $AaBb$.

But by reason of the dominance of one character of each pair these first crosses were hardly if at all distinguishable from AB.

By letting these $AaBb$'s fertilise themselves, only *four* classes of offspring seemed to be produced, namely,

AB	showing	both dominant characters.
Ab	,,	dominant A and recessive b.
aB	,,	recessive a and dominant B.
ab	,,	both recessive characters a and b.

The numerical ratios in which these classes appeared were also regular and approached the ratio

$$9AB : 3Ab : 3aB : 1ab.$$

But on cultivating these plants and allowing them to fertilise themselves it was found that the members of the

Ratios		
1		ab class produce only ab's.
3	1	aB class may produce either all aB's,
	2	*or* both aB's and ab's.
3	1	Ab class may produce either all Ab's,
	2	*or* both Ab's and ab's.
9	1	AB class may produce either all AB's,
	2	*or* both AB's and Ab's,
	2	*or* both AB's and aB's,
	4	*or* all four possible classes again, namely, AB's, Ab's, aB's, and ab's,

and the average number of members of each class will approach the ratio 1 : 3 : 3 : 9 as indicated above.

The details of these experiments and of others like them made with *three* pairs of differentiating characters are all set out in Mendel's memoir.

Professor de Vries has worked at the same problem in some dozen species belonging to several genera, using pairs of varieties characterised by a great number of characters: for instance, colour of flowers, stems, or fruits, hairiness, length of style, and so forth. He states that in all these cases Mendel's principles are followed.

The numbers with which Mendel worked, though large, were not

large enough to give really smooth results[1]; but with a few rather marked exceptions the observations are remarkably consistent, and the approximation to the numbers demanded by the law is greatest in those cases where the largest numbers were used. When we consider, besides, that Tschermak and Correns announce definite confirmation in the case of *Pisum*, and de Vries adds the evidence of his long series of observations on other species and orders, there can be no doubt that Mendel's law is a substantial reality; though whether some of the cases that depart most widely from it can be brought within the terms of the same principle or not, can only be decided by further experiments.

One may naturally ask, How can these results be brought into harmony with the facts of hybridisation hitherto known; and, if all this is true, how is it that others who have carefully studied the phenomena of hybridisation have not long ago perceived this law? The answer to this question is given by Mendel at some length, and it is, I think, satisfactory. He admits from the first that there are undoubtedly cases of hybrids and cross-breds which maintain themselves pure and do not break up. Such examples are plainly outside the scope of his law. Next he points out, what to anyone who has rightly comprehended the nature of discontinuity in variation is well known, that the variations in *each* character must be *separately* regarded. In most experiments in crossing, forms are taken which differ from each other in a multitude of characters—some continuous, others discontinuous, some capable of blending with their contraries, while others are not. The observer on attempting to perceive any regularity is confused by the complications thus introduced. Mendel's law, as he fairly says, could only appear in such cases by the use of overwhelming numbers, which are beyond the possibilities of practical experiment. Lastly, no previous observer had applied a strict statistical method.

Both these answers should be acceptable to those who have studied the facts of variation and have appreciated the nature of Species in the light of those facts. That different species should follow different laws, and that the same law should not apply to all characters alike, is exactly what we have every right to expect. It will also be remem-

[1] Professor Weldon (*Biometrika*, I, 1902, p. 232) takes great exception to this statement, which he considerately attributes to "some writers." After examining the conclusions he obtained by algebraical study of Mendel's figures I am disposed to think my statement not very far out.

bered that the principle is only explicitly declared to apply to discontinuous characters[1]. As stated also it can only be true where reciprocal crossings lead to the same result. Moreover, it can only be tested when there is no sensible diminution in fertility on crossing.

Upon the appearance of de Vries' paper announcing the "re-discovery" and confirmation of Mendel's law and its extension to a great number of cases, two other observers came forward almost simultaneously and independently described series of experiments fully confirming Mendel's work. Of these papers the first is that of Correns, who repeated Mendel's original experiment with Peas having seeds of different colours. The second is a long and very valuable memoir of Tschermak, which gives an account of elaborate researches into the results of crossing a number of varieties of *Pisum sativum*. These experiments were in many cases carried out on a large scale, and prove the main fact enuntiated by Mendel beyond any possibility of contradiction. The more exhaustive of these researches are those of Tschermak on Peas and Correns on several varieties of Maize. Both these elaborate investigations have abundantly proved the general applicability of Mendel's law to the character of the plants studied, though both indicate some few exceptions. The details of de Vries' experiments are promised in the second volume of his most valuable *Mutationstheorie*. Correns in regard to Maize and Tschermak in the case of *P. sativum* have obtained further proof that Mendel's law holds as well in the case of varieties differing from each other in *two* pairs of characters, one of each pair being dominant, though of course a more complicated expression is needed in such cases[2].

That we are in the presence of a new principle of the highest importance is manifest. To what further conclusions it may lead us cannot yet be foretold. But both Mendel and the authors who have followed him lay stress on one conclusion, which will at once suggest itself to anyone who reflects on the facts. For it will be seen that the results are such as we might expect if it be imagined that the cross-bred plant produced pollen grains and egg cells, each of which bears only *one* of the alternative varietal characters and not both. If this were so, and if on an average the same number of pollen grains and egg cells transmit each of the two characters, it is clear that on a

[1] See later.

[2] Tschermak's investigations were besides directed to a re-examination of the question of the absence of beneficial results on cross-fertilising *P. sativum*, a subject already much investigated by Darwin, and upon this matter also important further evidence is given in great detail.

random assortment of pollen grains and egg cells Mendel's law would be obeyed. For 25 per cent. of "dominant" pollen grains would unite with 25 per cent. "dominant" egg cells; 25 per cent. "recessive" pollen grains would similarly unite with 25 per cent. "recessive" egg cells; while the remaining 50 per cent. of each kind would unite together. It is this consideration which leads both Mendel and those who have followed him to assert that these facts of crossing prove that each egg cell and each pollen grain is pure in respect of each character to which the law applies. It is highly desirable that varieties differing in the form of their pollen should be made the subject of these experiments, for it is quite possible that in such a case strong confirmation of this deduction might be obtained. [Preliminary trials made with reference to this point have so far given negative results. Remembering that a pollen grain is not a germ cell, but only a bearer of a germ cell, the hope of seeing pollen grains differentiated according to the characters they bear is probably remote. Better hopes may perhaps be entertained in regard to spermatozoa, or possibly female cells.]

As an objection to the deduction of purity of germ cells, however, it is to be noted that though true intermediates did not generally occur, yet the intensity in which the characters appeared did vary in degree, and it is not easy to see how the hypothesis of *perfect* purity in the reproductive cells can be supported in such cases. Be this, however, as it may, there is no doubt we are beginning to get new lights of a most valuable kind on the nature of heredity and the laws which it obeys. It is to be hoped that these indications will be at once followed up by independent workers. Enough has been said to show how necessary it is that the subjects of experiment should be chosen in such a way as to bring the laws of heredity to a real test. For this purpose the first essential is that the differentiating characters should be few, and that all avoidable complications should be got rid of. Each experiment should be reduced to its simplest possible limits. The results obtained by Galton, and also the new ones especially described in this paper, have each been reached by restricting the range of observation to one character or group of characters, and it is certain that by similar treatment our knowledge of heredity may be rapidly extended.

To the above popular presentation of the essential facts, made for an audience not strictly scientific, some addition, however brief, is called for. First, in regard to the law of Ancestry, spoken of on p. 7.

Those who are acquainted with Pearson's *Grammar of Science*, 2nd ed. published early in 1900, the same author's paper in *Proc. Roy. Soc.* LXVI, 1900, p. 140, or the extensive memoir (pubd. Oct. 1900) on the inheritance of coat-colour in horses and eye-colour in man (*Phil. Trans.* CXCV, A, 1900, p. 79), will not need to be told that the few words I have given above constitute a most imperfect diagram of the operations of that law as now developed. Until the appearance of these treatises it was, I believe, generally considered that the law of Ancestral Heredity was to be taken as applying to phenomena like these (coat-colour, eye-colour, etc.) where the inheritance is generally *alternative*, as well as to the phenomena of *blended* inheritance.

Pearson, in the writings referred to, besides withdrawing other large categories of phenomena from the scope of its operations, points out that the law of Ancestral Heredity does not satisfactorily express the cases of alternative inheritance. He urges, and with reason, that these classes of phenomena should be separately dealt with.

The whole issue as regards the various possibilities of heredity now recognised will be made clearer by a very brief exposition of the several conceptions involved.

If an organism producing germ cells of a given constitution, uniform in respect of the characters they bear, breeds with another organism[1] bearing *precisely similar* germ cells, the offspring resulting will, if the conditions are identical, be uniform.

In practice such a phenomenon is seen in *pure*-breeding. It is true that we know no case in nature where all the germ cells are thus identical, and where no variation takes place beyond what we can attribute to conditions, but we know many cases where such a result is approached, and very many where all the essential features which we regard as constituting the characters of the breed are reproduced with approximate certainty in every member of the pure-bred race, which thus closely approach to uniformity.

But if two germ cells of dissimilar constitution unite in fertilisation, what offspring are we to expect[2]? First let us premise that the answer to this question is known experimentally to differ for many organisms and for many classes of characters, and may almost certainly be in part determined by external circumstances. But omitting the last

[1] For simplicity the case of self-fertilisation is omitted from this consideration.

[2] In all the cases discussed it is assumed that the gametes are similar except in regard to the "heritage" they bear, and that no *original* variation is taking place. The case of mosaics is also left wholly out of account (see later).

qualification, certain principles are now clearly detected, though what principle will apply in any given case can only be determined by direct experiment made with that case.

This is the phenomenon of *cross*-breeding. As generally used, this term means the union of members of dissimilar varieties, or species: though when dissimilar gametes[1] produced by two individuals of the same variety unite in fertilisation, we have essentially *cross*-breeding in respect of the character or characters in which those gametes differ. We will suppose, as before, that these two gametes bearing properties unlike in respect of a given character, are borne by different individuals.

In the simplest case, suppose a gamete from an individual presenting any character in intensity A unite in fertilisation with another from an individual presenting the same character in intensity a. For brevity's sake we may call the parent individuals A and a, and the resulting zygote Aa. What will the structure of Aa be in regard to the character we are considering?

Up to Mendel no one proposed to answer this question in any other way than by reference to the intensity of the character in the progenitors, and *primarily* in the parents, A and a, in whose bodies the gametes had been developed. It was well known that such a reference gave a very poor indication of what Aa would be. Both A and a may come from a population consisting of individuals manifesting the same character in various intensities. In the pedigree of either A or a these various intensities may have occurred few or many times. Common experience leads us to expect the probability in regard to Aa to be influenced by this history. The next step is that which Galton took. He extended the reference beyond the immediate parents of Aa, to its grandparents, great-grandparents, and so on, and in the cases he studied he found that from a knowledge of the intensity in which the given character was manifested in each progenitor, even for some few generations back, a fairly accurate prediction could be made, not as to the character of any individual Aa, but as to the average character of Aa's of similar parentage, in general.

But suppose that instead of individuals presenting one character in differing intensities, two individuals breed together distinguished by characters which we know to be mutually exclusive, such as A

[1] The term "gamete" is now generally used as the equivalent of "germ cell," whether male or female, and the term "zygote" is here used for brevity to denote the organism resulting from fertilisation.

and B. Here again we may speak of the individuals producing the gametes as A and B, and the resulting zygote as AB. What will AB be like? The population here again may consist of many like A and like B. These two forms may have been breeding together indiscriminately, and there may have been many or few of either type in the pedigree of either A or B.

Here again Galton applied his method with remarkable success. Referring to the progenitors of A and B, determining how many of each type there were in the direct pedigree of A and B, he arrived at the same formula as before, with the simple difference that instead of expressing the probable average intensity of one character in several individuals, the prediction is given in terms of the probable number of A's and B's that would result on an average when particular A's and B's of known pedigree breed together.

The law as Galton gives it is as follows:

"It is that the two parents contribute between them on the average one-half, or (0·5) of the total heritage of the offspring; the four grandparents, one-quarter, or $(0{\cdot}5)^2$; the eight great-grandparents, one-eighth, or $(0{\cdot}5)^3$, and so on. Then the sum of the ancestral contributions is expressed by the series

$$\{(0{\cdot}5) + (0{\cdot}5)^2 + (0{\cdot}5)^3, \text{etc.}\},$$

which, being equal to 1, accounts for the whole heritage."

In the former case, where A and a are characters which can be denoted by reference to a common scale, the law assumes of course that the inheritance will be, to use Galton's term, *blended*, namely that the zygote resulting from the union of A with a will on the average be more like a than if A had been united with A; and conversely that an Aa zygote will on the average *be more like A than an aa zygote would be.*

But in the case of A's and B's, which are assumed to be mutually exclusive characters, we cannot speak of blending, but rather, to use Galton's term, of *alternative* inheritance.

Pearson, finding that the law whether formulated thus, or in the modified form in which he restated it[1], did not express the phenomena of alternative inheritance known to him with sufficient accuracy to justify its strict application to them, and also on general grounds, proposed that the phenomena of blended and alternative inheritance

[1] In Pearson's modification the parents contribute 0·3, the grandparents 0·15, the great-grandparents 0·075.

should be treated apart—a suggestion[1] the wisdom of which can scarcely be questioned.

Now the law thus imperfectly set forth and every modification of it is incomplete in one respect. It deals only with the characters of the resulting zygotes and predicates nothing in regard to the gametes which go to form them. A good prediction may be made as to any given group of zygotes, but the various possible constitutions of the gametes are not explicitly treated.

Nevertheless a definite assumption is implicitly made regarding the gametes. It is not in question that differences between these gametes may occur in respect of the heritage they bear; yet it is assumed that these differences will be distributed among the gametes of any individual zygote in such a way that each gamete remains capable, on fertilisation, of transmitting *all* the characters (both of the parent-zygote and of its progenitors) to the zygote which it then contributes to form (and to the posterity of that zygote) in the intensity indicated by the law. Hence the gametes of any individual are taken as collectively a fair sample of all the racial characters in their appropriate intensities, and this theory demands that there shall have been no qualitative redistribution of characters among the gametes of any zygote in such a way that some gametes shall be finally excluded from partaking of and transmitting any specific part of the heritage. The theory further demands—and by the analogy of what we know otherwise not only of animals and plants, but of physical or chemical laws, perhaps this is the most serious assumption of all—that the structure of the gametes shall admit of their being capable of transmitting any character in any intensity varying from zero to totality with equal ease; and that gametes of each intensity are all equally likely to occur, given a pedigree of appropriate arithmetical composition.

Such an assumption appears so improbable that even in cases where the facts seem as yet to point to this conclusion with exceptional clearness, as in the case of human stature, I cannot but feel there is still room for reserve of judgment.

However this may be, the Law of Ancestral Heredity, and all modifications of it yet proposed, falls short in the respect specified above, that *it does not directly attempt to give any account of the distribution of the heritage among the gametes* of any one individual.

Mendel's conception differs fundamentally from that involved in

[1] See the works referred to above.

the Law of Ancestral Heredity. The relation of his hypothesis to the foregoing may be most easily shown if we consider it first in application to the phenomena resulting from the cross-breeding of two pure varieties.

Let us again consider the case of two varieties each displaying the same character, but in the respective intensities A and a. Each gamete of the A variety bears A, and each gamete of the a variety bears a. When they unite in fertilisation they form the zygote Aa. What will be its characters? The Mendelian teaching would reply that this can only be known by direct experiment with the two forms A and a, and that the characters A and a perceived in those two forms or varieties need not give any indication as to the character of the zygote Aa. It may display the character A, or a, or a character half way between the two, or a character beyond A or below a. The character of Aa is not regarded as a *heritage* transmitted to it by A and by a, but as a character special and peculiar to Aa, just as $NaCl$ is not a body half way between sodium and chlorine, or such that its properties can be predicted from or easily stated in terms of theirs.

If a concrete case may help, a tall pea A crossed with a dwarf a often produces, not a plant having the height of either A or a, but something *taller* than the pure tall variety A.

But if the case obeys the Mendelian principles—as does that here quoted—then it can be declared *first* that the gametes of Aa will not be bearers of the character proper to Aa; but, generally speaking, each gamete will either bear the pure A character or the pure a character. There will in fact be a redistribution of the characters brought in by the gametes which united to form the zygote Aa, such that each gamete of Aa is pure, as the parental gametes were. *Secondly*, this redistribution will occur in such a way that, of the gametes produced by such Aa's, on an average there will be equal numbers of A gametes and of a gametes.

Consequently if Aa's breed together, the new A gametes may meet each other in fertilisation, forming a zygote AA, namely, the pure A variety again; similarly two a gametes may meet and form aa, or the pure a variety again. But if an A gamete meets an a it will once more form Aa, with its special character. This Aa is the hybrid, or "mule" form, or, as I have elsewhere called it, the *heterozygote*, as distinguished from AA or aa the *homozygotes*.

Similarly, if the two gametes of two varieties distinguished by characters, A and B, which cannot be described in terms of any

common scale (such as, for example, the "rose" and "single" combs of fowls) unite in fertilisation, again the character of the mule form cannot be predicted. Before the experiment is made the "mule" may present *any* form. Its character or properties can as yet be no more predicted than could those of the compounds of unknown elements before the discovery of the periodic law.

But again—if the case be Mendelian—the gametes borne by AB will be either A's or B's[1], and the cross-bred AB's breeding together will form AA's, AB's and BB's. Moreover, if, as in the normal Mendelian case, AB's bear on an average equal numbers of A gametes and B gametes, the numerical ratio of these resulting zygotes to each other will be

$$1\,AA : 2\,AB : 1\,BB.$$

We have seen that Mendel makes no prediction as to the outward and visible characters of AB, but only as to the essential constitution and statistical condition of its gametes in regard to the characters A and B. Nevertheless, in a large number of cases the character of AB is known to fall into one of three categories (omitting mosaics).

(1) The cross-bred may almost always resemble one of its pure parents so closely as to be practically indistinguishable from that pure form, as in the case of the yellow cotyledon-colour of certain varieties of peas when crossed with green-cotyledoned varieties; in which case the parental character, yellow, thus manifested by the cross-bred is called "dominant" and the parental character, green, not manifested, is called recessive.

(2) The cross-bred may present some condition intermediate between the two parental forms, in which case we may still retain the term "blend" as applied to the zygote.

Such an "intermediate" may be the apparent mean between the two parental forms or be nearer to one or other in any degree. Such a case is that of a cross between a rich crimson Magenta Chinese Primrose and a clear White, giving a flower of a colour appropriately described as a "washy" magenta.

(3) The cross-bred may present some form quite different from that of either pure parent. Though, as has been stated, nothing can be

[1] This conception was clearly formed by Naudin (*Nouv. Arch. Mus.*, I, 1865) simultaneously with Mendel, but it was not worked out by him and remained a mere suggestion. In one place also Focke (*Oesterr. Bot. Ztschr.*, XVIII, 1868) came very near to the same idea.

predicted of an unknown case, we already know a considerable number of examples of this nature in which the mule-form *approaches sometimes with great accuracy to that of a putative ancestor, near or remote.* It is scarcely possible to doubt that several—though perhaps not all—of Darwin's "reversions on crossing" were of this nature.

Such a case is that of the "wild grey mouse" produced by the union of an albino tame mouse and a piebald Japanese mouse[1]. These "reversionary" mice bred together produce the parental tame types, some other types, and "reversionary" mice again.

From what has been said it will now be clear that the applicability of the Mendelian hypothesis has, intrinsically, nothing whatever to do with the question of the inheritance being *blended* or *alternative*. In fact, as soon as the relation of zygote characters to gamete characters is appreciated, it is difficult to see any reason for supposing that the manifestation of characters seen in the zygotes should give any indication as to their mode of allotment among the gametes.

On a previous occasion I pointed out that the terms "Heredity" and "Inheritance" are founded on a mis-application of metaphor, and in the light of our present knowledge it is becoming clearer that the ideas of "transmission" of a character by parent to offspring, or of there being any "contribution" made by an ancestor to its posterity, must only be admitted under the strictest reserve, and merely as descriptive terms.

We are now presented with some entirely new conceptions:

(1) Tbe purity of the gametes in regard to certain characters.

(2) The distinction of all zygotes according as they are or are not formed by the union of like or unlike gametes. In the former case, apart from Variation, they breed true when mated with their like; in the latter case their offspring, collectively, will be heterogeneous.

(3) If the zygote be formed by the union of dissimilar gametes, we may meet the phenomenon of (*a*) dominant and recessive characters; (*b*) a blend form; (*c*) a form distinct from either parent, often reversionary[2].

[1] See von Guaita, *Ber. naturf. Ges. Freiburg*, x, 1898 and xi, 1899, quoted by Professor Weldon.

[2] This fact sufficiently indicates the difficulties involved in a superficial treatment of the phenomenon of reversion. To call such reversions as those named above "returns to ancestral type" would be, if more than a descriptive phrase were intended, quite misleading. It is not the ancestral *type* that has come back, but something else has come in its guise, as the offspring presently prove. For the first time we thus begin to get a rationale of "reversion."

But there are additional and even more significant deductions from the facts. We have seen that the gametes are differentiated in respect of pure characters. Of these pure characters there may *conceivably* be any number associated together in one organism. In the pea Mendel detected at least seven—not all seen by him combined in the same plant, but there is every likelihood that they are all capable of being thus combined.

Each such character, which is capable of being dissociated or replaced by its contrary, must henceforth be conceived of as a distinct *unit-character*; and as we know that the several unit-characters are of such a nature that any one of them is capable of independently displacing or being displaced by one or more alternative characters taken singly, we may recognise this fact by naming such unit-characters *allelomorphs*. So far, we know very little of any allelomorphs existing otherwise than as *pairs* of contraries, but this is probably merely due to experimental limitations and the rudimentary state of our knowledge.

In one case (combs of fowls) we know three characters—*pea* comb, *rose* comb and *single* comb; of which *pea* and *single*, or *rose* and *single*, behave towards each other as a pair of allelomorphs, but of the behaviour of *pea* and *rose* towards each other we know as yet nothing.

We have no reason as yet for affirming that any phenomenon properly described as *displacement* of one allelomorph by another occurs, though the metaphor may be a useful one. In all cases where *dominance* has been perceived, we can affirm that the members of the allelomorphic pair stand to each other in a relation the nature of which we are as yet wholly unable to apprehend or illustrate.

To the new conceptions already enumerated we may therefore add

(4) *Unit-characters* of which some, *when once arisen by Variation*, are alternative to each other in the constitution of the gametes, according to a definite system.

From the relations subsisting between these characters, it follows that as each zygotic union of allelomorphs is *resolved* on the formation of the gametes, no zygote can give rise to gametes collectively representing more than *two* characters allelomorphic to each other, apart from new variation.

From the fact of the existence of the interchangeable characters we must, for purposes of treatment, and to complete the possibilities, necessarily form the conception of an *irresoluble base*, though whether

such a conception has any objective reality we have no means as yet of determining.

We have now seen that when the varieties A and B are crossed together, the heterozygote, AB, produces gametes bearing the pure A character and the pure B character. In such a case we speak of such characters as *simple* allelomorphs. In many cases however a more complex phenomenon happens. The character brought in on fertilisation by one or other parent may be of such a nature that when the zygote, AB, forms its gametes, these are not individually bearers merely of A and B, *but of a number of characters themselves again integral*, which in, say, A behaved as one character so long as its gametes united in fertilisation with others like themselves, but on cross-fertilisation are resolved and redistributed among the gametes produced by the cross-bred zygote.

In such a case we call the character A a *compound* allelomorph, and we can speak of the integral characters which constitute it as *hypallelomorphs*. We ought to write the heterozygote $(AA'A''...)B$ and the gametes produced by it may be of the form $A, A', A'', A''',...B$. Or the resolution may be incomplete in various degrees, as we already suspect from certain instances; in which case we may have gametes A, $A'A''$, $A'''A''''$, $A'A''A^{v}$,...B, and so on. Each of these may meet a similar or a dissimilar gamete in fertilisation, forming either a homozygote, or a heterozygote with its distinct properties.

In the case of compound allelomorphs we know as yet nothing of the statistical relations of the several gametes.

Thus we have the conception

(5) *of a Compound character*, borne by one gamete, transmitted entire as a single character so long as fertilisation only occurs between like gametes, or is, in other words, "symmetrical," but if fertilisation take place with a dissimilar gamete (or possibly by other causes), resolved into integral constituent-characters, each separately transmissible.

Next, as, by the union of the gametes bearing the va ous hypallelomorphs with other such gametes, or with gametes bearing simple allelomorphs, in fertilisation, a number of new zygotes will be formed, such as may not have been seen before in the breed: these will inevitably be spoken of as *varieties*; and it is difficult not to extend the idea of variation to them. To distinguish these from other variations—which there must surely be—we may call them

(6) *Analytical* variations in contradistinction to

(7) *Synthetical* variations, occurring not by the separation of pre-existing constituent-characters but by the addition of new characters.

Lastly, it is impossible to be presented with the fact that in Mendelian cases the cross-bred produces on an average *equal* numbers of gametes of each kind, that is to say, a symmetrical result, without suspecting that this fact must correspond with some symmetrical figure of distribution of those gametes in the cell-divisions by which they are produced.

At the present time these are the main conceptions—though by no means all—arising directly from Mendel's work. The first six are all more or less clearly embodied by him, though not in every case developed in accordance with modern knowledge. The seventh is not a Mendelian conception, but the facts before us justify its inclusion in the above list though for the present it is little more than a mere surmise.

In Mendelian cases it will now be perceived that all the zygotes composing the population consist of a limited number of possible types, each of definite constitution, bearing gametes also of a limited and definite number of types, and definite constitution in respect of pre-existing characters. It is now evident that in such cases each several progenitor need not be brought to account in reckoning the probable characters of each descendant; for the gametes of cross-breds are differentiated at each successive generation, some parental (Mendelian) characters being left out in the composition of each gamete produced by a zygote arising by the union of bearers of opposite allelomorphs.

When from these considerations we return to the phenomena comprised in the Law of Ancestral Heredity, what certainty have we that the same conceptions are not applicable there also?

It has now been shown that the question whether in the cross-bred zygotes in general the characters blend or are mutually exclusive is an entirely subordinate one, and distinctions with regard to the essential nature of heredity based on these circumstances become irrelevant.

In the case of a population presenting continuous variation in regard to, say, stature, it is easy to see how purity of the gametes in respect of any intensities of that character might not in ordinary circumstances be capable of detection. There are doubtless more than two pure gametic forms of this character, but there may quite con-

ceivably be six or eight. When it is remembered that each heterozygous combination of any two may have its own appropriate stature, and that such a character is distinctly dependent on external conditions, the mere fact that the observed curves of stature give "chance distributions" is not surprising and may still be compatible with purity of gametes in respect of certain pure types. In Peas (*P. sativum*), for example, from Mendel's work we know that the tall forms and the extreme dwarf forms exhibit gametic purity. I have seen at Messrs Sutton's strong evidence of the same nature in the case of the tall Sweet Pea (*Lathyrus odoratus*) and the dwarf or procumbent "Cupid" form.

But in the case of the Sweet Pea we know at least one pure form of definitely intermediate height, and in the case of *P. sativum* there are many. When the *extreme* types breed together it will be remembered the heterozygote commonly exceeds the taller in height. In the next generation, since there is, in the case of extremes, so much margin between the types of the two pure forms, the return of the offspring to the three forms of which two are homozygous and one heterozygous is clearly perceptible.

If however instead of pure extreme varieties we were to take a pair of varieties differing normally by only a foot or two, we might, owing to the masking effects of conditions, etc., have great difficulty in distinguishing the three forms in the second generation. There would besides be twice as many heterozygous individuals as homozygous individuals of each kind, giving a symmetrical distribution of heights, and who might not—in pre-Mendelian days—have accepted such evidence—made still less clear by influence of conditions—as proof of Continuous Variation both of zygotes and gametes?

Suppose, then, that instead of two pure types, we had six or eight breeding together, each pair forming their own heterozygote, there would be a very remote chance of such purity or fixity of type, whether of gamete or zygote, being detected.

Dominance, as we have seen, is merely a phenomenon incidental to specific cases, between which no other common property has yet been perceived. In the phenomena of *blended* inheritance we clearly have no dominance. In the cases of *alternative* inheritance studied by Galton and Pearson there is evidently no *universal* dominance. From the tables of Basset hound pedigrees there is clearly no definite dominance of either of the coat-colours. In the case of eye-colour the published tables do not, so far as I have discovered, furnish the material

for a decision, though it is scarcely possible the phenomenon, even if only occasional, could have been overlooked. We must take it, then, there is no sensible dominance in these cases; but whether there is or is not sensible gametic purity is an altogether different question, which, so far as I can judge, is as yet untouched. It may perfectly well be that we shall be compelled to recognise that in many cases there is no such purity, and that the characters may be carried by the gametes in any proportion from zero to totality, just as some substances may be carried in a solution in any proportion from zero to saturation without discontinuous change of properties. That this will be found true in *some* cases is, on any hypothesis, certain; but to prove the fact for any given case will be an exceedingly difficult operation, and I scarcely think it has been yet carried through in such a way as to leave no room for doubt.

Conversely, the *absolute* and *universal* purity of the gametes has certainly not yet been determined for any case; not even in those cases where it looks most likely that such universal purity exists. Impairment of such purity we may conceive either to occur in the form of mosaic gametes, or of gametes with blended properties. On analogy and from direct evidence we have every right to believe that gametes of both these classes may occur in rare and exceptional cases, of as yet unexplored nature[1], but such a phenomenon will not diminish the significance of observed purity.

We have now seen the essential nature of the Mendelian principles and are able to appreciate the exact relation in which they stand to the group of cases included in the Law of Ancestral Heredity. In seeking any general indication as to the common properties of the phenomena which are already known to obey Mendelian principles we can as yet point to none, and whether some such common features exist or not is unknown.

There is however one group of cases, definite though as yet not numerous, where we know that the Mendelian principles do not apply. These are the phenomena upon which Mendel touches in his brief paper on *Hieracium*. As he there states, the hybrids, if they are fertile at all, produce offspring like themselves, not like their parents. In further illustration of this phenomenon he cites Wichura's *Salix* hybrids. Perhaps some dozen other such illustrations could be given which rest on good evidence. To these cases the Mendelian principle

[1] It will be understood from what follows, that the existence of mosaic zygotes is no *proof* that either component gamete was mosaic.

will in nowise apply, nor is it easy to conceive any modification of the law of ancestral heredity which can express them. There the matter at present rests. Among these cases, however, we perceive several more or less common features. They are often, though not always, hybrids between forms differing in many characters. The first cross frequently is not the exact intermediate between the two parental types, but may, as in the few *Hieracium* cases, be irregular in this respect. There is often some degree of sterility. In the absence of fuller and statistical knowledge of such cases further discussion is impossible.

Another class of cases, untouched by any hypothesis of heredity yet propounded, is that of the false hybrids of Millardet, where we have fertilisation without transmission of one or several parental characters. In these not only does the first cross show, in some respect, the character or characters of *one parent only*, but in its posterity *no reappearance of the lost character or characters is observed.* The nature of such cases is still quite obscure, but we have to suppose that the allelomorph of one gamete only developes after fertilisation to the exclusion of the corresponding allelomorph of the other gamete, much—if the crudity of the comparison may be pardoned—as occurs on the female side in parthenogenesis without fertilisation at all.

To these as yet altogether unconformable cases we can scarcely doubt that further experiment will add many more. Indeed, we already have tolerably clear evidence that many phenomena of inheritance are of a much higher order of complexity. When the paper on *Pisum* was written Mendel apparently inclined to the view that with modifications his law might be found to include all the phenomena of hybridisation, but in the brief subsequent paper on *Hieracium* he clearly recognised the existence of cases of a different nature. Those who read that contribution will be interested to see that he lays down a principle which may be extended from hybridisation to heredity in general, that the laws of each new case must be determined by separate experiment.

As regards the Mendelian principles, which it is the chief aim of this introduction to present clearly before the reader, a professed student of variation will easily be able to fill in the outline now indicated, and to illustrate the various conceptions from phenomena already familiar. To do this is beyond the scope of this short sketch. But enough perhaps has now been said to show that by the application of those principles we are enabled to reach and deal in

a comprehensive manner with phenomena of a fundamental nature, lying at the very root of all conceptions not merely of the physiology of reproduction and heredity, but even of the essential nature of living organisms; and I think that I used no extravagant words when, in introducing Mendel's work to the notice of readers of the Royal Horticultural Society's Journal, I ventured to declare that his experiments are worthy to rank with those which laid the foundation of the Atomic laws of Chemistry.

THE FACTS OF HEREDITY IN THE LIGHT OF MENDEL'S DISCOVERY

[*Reports to the Evolution Committee of the Royal Society*, I, 1902, pp. 125–160]

As was stated in the introduction to this paper, with the discovery of the Mendelian principle the problem of evolution passes into a new phase. It is scarcely possible to overrate the importance of this discovery. Every conception of biology which involves a knowledge of the physiology of reproduction must feel the influence of the new facts, and, in their light, previous ideas of heredity and variation, the nature of specific differences, and all that depends on those ideas must be reconsidered, and in great measure modified.

If we turn to any former description of breeding experiments we generally perceive at once that the whole account must be re-stated in terms of Mendel's hypothesis, and that the discussions and arguments based on former hypotheses are now meaningless. As an illustration we may take the account which Darwin gives of his experiments with peloric Antirrhinum[1]. He crossed the peloric form with the normal and *vice versâ*. The first crosses were all indistinguishable from the normal or zygomorphic form. These were allowed to fertilise themselves, and gave a crop consisting of 88 normals, 2 intermediates, and 37 perfectly peloric. He discusses these results on the hypothesis that the normal plant has a "tendency" to become peloric, and the peloric a "tendency" to become normal, "so that we have two opposed latent tendencies in the same plants. Now with the crossed Antirrhinums the tendency to produce normal or irregular flowers, like those of the common Snapdragon, prevailed in the first generation; whilst the tendency to pelorism, appearing to gain strength by the intermission of a generation, prevailed to a large extent in the second set of seedlings. How it is possible for a character to gain strength by the intermission of a generation will be considered in the chapter on pangenesis."

Now, of course, we can perceive that the zygomorphic form is dominant and the peloric recessive, and that the arguments based on other hypotheses have no longer any significance. It would be a useful task to go similarly through the literature of breeding and translate the results into Mendelian terms. Such an exercise would

[1] *Animals and Plants*, II, p. 46, ed. 1885.

show that the change which must now come over the conceptions of biology can only be compared with that which in the study of physical science followed the revelations of modern chemistry.

The outcome of such a revision of current conceptions it is impossible to foresee, but we propose in the present paper to consider some of the more important questions which are immediately raised.

To denote the new conceptions some new terms are needed. Several have already been suggested by Correns, but in practice we have not found his terminology altogether convenient, or that it meets the new requirements. Correns proposes the terms "heterodynamous" and "homodynamous" to express that an organism is dominant or not dominant in respect of a given character. There are unfortunately objections to the use of these terms, though in some respects they are very suitable. First, they are in use by Weismann and his followers in quite different senses, as Correns states. Secondly, it is not clear whether they are to be applied to the variety, the individual, or the character. Besides these objections, it is fairly clear that dominance is a phenomenon presenting various degrees of intensity; and while the single phenomenon of dominance is well expressed by that word itself, other conditions probably consist of various phenomena which are not conveniently denoted by one word.

Correns' terms "homoögonous" and "schizogonous" cannot as yet be used with precision to mean more than breeding "true" and not breeding "true," and, for reasons given later, the metaphor of splitting may be incorrect.

The terms also "*halb-identisch*" and "*conjugirte*" as applied to characters, are already fairly well expressed hy the words in perfect or in imperfect correlation, which are already well understood. It would be confusing to introduce the metaphor of conjugation to denote these ideas.

But while doubting whether this terminology already suggested will be found adequate, we do not propose at present to substitute new terms for the same phenomena. In our view, there are other conceptions arising from the Mendelian discoveries for which brief expressions are absolutely required, and for these we suggest the following terminology.

In the introduction (R. p. 12)[1] we attempted to distinguish precisely the essential fact discovered by Mendel, and to separate it from other subordinate appearances. We may now briefly recall and amplify

[1] [R. prefixed denotes pagination in original Report. ED.]

that reasoning, showing how we propose to denote the several phenomena.

By crossing two forms exhibiting antagonistic characters, cross-breds were produced. The generative cells of these cross-breds were shown to be of two kinds, each being pure in respect of *one* of the parental characters. This purity of the germ cells, and their inability to transmit both of the antagonistic characters, is the central fact proved by Mendel's work. We thus reach the conception of unit-characters existing in antagonistic pairs. Such characters we propose to call *allelomorphs*[1], and the zygote formed by the union of a pair of opposite allelomorphic gametes we shall call a *heterozygote*. Similarly, the zygote formed by the union of gametes having similar allelomorphs, may be spoken of as a *homozygote*. Upon a wide survey, we now recognise that this first principle has an extensive application in nature. We cannot as yet determine the limits of its applicability, and it is possible that many characters may really be allelomorphic, which we now suppose to be "transmissible" in any degree or intensity. On the other hand, it is equally possible that characters found to be allelomorphic in some cases may prove to be non-allelomorphic in others.

It will be of great interest to determine how far the purity of the germ cells in respect of allelomorphic characters is an absolute rule, or whether there are exceptional cases in which such purity may be impaired. That such exceptions may arise is indeed almost certain from the evidence of "mosaic" fruits in *Datura*, where it was shown (R. p. 23) that the otherwise pure extracted recessives (thornless) showed exceptionally a thorny patch or segment. Unless this is an original sport on the part of the individual, such a phenomenon may be taken as indicating that the germ cells may also have been mosaic[2]. Indeed, all that we know of the occurrence and distribution of variation among repeated parts, would lead us to expect such a possibility with confidence.

This is a question we can analyse no further. Were it possible to do so, it might be a real help towards getting a picture of the actual process of heredity.

But besides the strictly allelomorphic or Mendelian distribution of characters among the gametes (with or without mosaics), we can

[1] Correns speaks of the two opposite allelomorphs as a *Paarling*.

[2] Conceivably the cases of poultry having one foot with extra toe and one normal, may be of a similar nature, though for various reasons this is unlikely.

imagine three other possible arrangements. (1) There may be a substantial discontinuity, the two types of gamete being connected by a certain proportion of intermediates, such as are often met with in cases even of almost complete discontinuity among zygotes. (2) There may be continuous variation among the gametes, shading from gametes pure to the one type, to gametes pure to the other type, the intermediates being the most frequent. (3) There may be no differentiation among the gametes in respect of parental characters at all, each representing the heterozygote characters unresolved. This last is the homoögonous type of Correns. By a sufficiently wide survey, illustrations of each of these systems and of intermediates between them, will doubtless be found, and the classification of gametic differentiation according to these several types, in respect of various characters, in various species, will be a first step towards the construction of a general scheme of heredity.

In gametic variation we thus meet in fact the same series of possibilities with which we have been familiar in the variation of zygotic organisms.

The second fact observed by Mendel is that each heterozygote produces on an average equal numbers of gametes bearing each allelomorph of each pair. This is only enunciated as an *average* result. Unfortunately, the determinations of the results for individuals are still few, but from those that have been made, and even from the few recorded by Mendel himself, we see that the fluctuations are so great, that we must suspect some special sources of disturbance. Contributing to the average result of 3 : 1 as between round and wrinkled peas, he mentions as extremes 43 : 2, 14 : 15; and between yellow and green 20 : 19 and 32 : 1. It is obvious that this suggests either that there has been for some cause selection among the germ cells originally equal in numbers, or that the numbers were originally unequal, or that the assortment of male and female germs was not governed by pure chance. Probably a series of individual determinations when seriated would throw light on the nature of these remarkable fluctuations which have been observed in almost all the subjects studied. From what we already know (R. p. 121), in respect of the output of the two kinds of gametes, it is fairly certain that fluctuations take place, corresponding probably with changes in health, age, and other conditions.

From analogy—an unsafe guide in these fields—and from what is known of discontinuous variation in general, we incline to the view

that even though the figures point to a sharp discontinuity between dominant and recessive elements, we shall ultimately recognise that the discontinuity between these elements need not be *universally* absolute. We may expect to find individuals, and perhaps breeds or strains, and even individual gonads or groups of gonads, in which the discontinuity is less sharp even in respect of these very characters; similarly, for such units definite departures from statistical equality between *D* and *R* germs may be expected. In *Pisum*, for instance, we cannot be far out in considering an average of 50 per cent. *D* and 50 per cent. *R* as a close approximation to the truth for both male and female cells, but there is nothing yet which proves even here that the discontinuity *must be always and absolutely complete*.

Similarly, we are not compelled to accept the proposition that germ cells of each allelomorph *always* exist on an average in equal numbers. The proofs of the two propositions are unfortunately as yet interdependent. The purity of the extracted recessives and dominants has been tested, and we can in such cases accept it as a fact: the *universal* purity of the gametes we cannot test. For, any dominant which gives rise to a recessive offspring we should class as a cross-bred, because cross-breds are like dominants in appearance. Similarly, any partially impure recessive would be classed as a cross-bred. If the number of germs of each kind borne by the cross-bred is sensibly unequal, or the discontinuity between them sensibly lessened, we can perceive a result, but we shall not know to which cause to ascribe it. The statistical method unfortunately cannot distinguish between the two causes in such a case. Readers of Mendel's paper will be aware that he laid down no universal rule as to the absolute purity of gametes, but merely pointed out that his results were explicable on the hypothesis of such purity.

The statistics, however, are not so precise as to compel us to accept *both* that the germs of the cross-breds are *always* pure, and that they are *always* produced on an average in equal numbers.

The next point arising immediately out of Mendel's work concerns the characters of the heterozygote. In the *Pisum* cases the heterozygote normally exhibits only one of the allelomorphs clearly, which is therefore called the dominant. It is, however, clear from what we know of cross-breeding, that such exclusive exhibition of one allelomorph in its totality is by no means a universal phenomenon. Even in the pea it is not the case that the heterozygote always shows the dominant allelomorph as clearly and in the same intensity as the

pure dominant, and speaking generally, heterozygotes, though in numerous instances readily referable to one or other of the allelomorphic types, exhibit those types in a more or less modified form.

Besides these, there are undoubtedly cases in which the heterozygote may show *either* of the allelomorphs, though one is commonly dominant. In the poultry crosses it was shown that the usually recessive foot-character (want of extra toe) may appear in the cross-bred. The want of dominance of hoariness in *Matthiola* seen in exceptional cases is a wholly different phenomenon (see R. pp. 45 and 79).

From the analogy of poultry, it is scarcely doubtful that polydactylism in man is also allelomorphic to the normal, and here from the tables of heredity already recorded[1], there is good evidence that both the normal and the polydactyle offspring of one polydactyle parent can transmit the polydactylism; in other words, the heterozygote may exhibit either allelomorph. Cases of the same phenomenon can indeed be multiplied. It must, however, be remembered that what is accepted as evidence of alternative inheritance, is not a proof that the dominance of either allelomorph is imperfect. This can only be known for certain when it has already been established that individuals showing either of the two allelomorphs can, when mated with an individual showing the same allelomorph, produce both allelomorphs among their offspring[2].

This leads to a point of great importance to the evolutionist. We have been in the habit of speaking of a variation as discontinuous, in proportion as between it and other forms of the species intermediates are comparatively scarce when all breed freely together. In all cases of allelomorphic characters we can now give a more precise meaning to this description. It must now be recognised that such a population consists, in respect of each pair of allelomorphs, of *three*[3] *kinds of individuals*, namely, homozygotes containing one allelomorph, homozygotes containing the other allelomorph, and heterozygotes compounded of both. The first two will thus always form discontinuous groups, and the degree to which the heterozygotes form a connecting group, will depend on whether one allelomorph regularly

[1] For examples see Fackenheim, *Jen. Zt.*, XXII, p. 343.

[2] For the present, therefore, we are not entitled to assume that the numerous cases among *Lepidoptera* of varieties breeding together with a discontinuous mixed result are allelomorphic, probable as this conclusion is. Such cases are those of *Amphidasys betularia* and *doubledayaria*; *Aglia tau* and *lugens*; *Angerona prunaria* and *sordiata Miana strigilis* and *æthiops*, etc. See Standfuss, *Handb. d. pal. Gross-Schmetterl.*, 1896, p. 305, *et seq.*

[3] Four, if reciprocal heterozygotes are not identical.

or chiefly dominates in the heterozygote, or the allelomorphic characters completely or partially blend in the heterozygote. *Such discontinuity will in fact primarily depend not on the blending or non-blending of the characters, as hitherto generally assumed, but on the permanent discontinuity or purity of the unfertilised germ cells.*

It will be of great interest to study the statistics of such a population in nature. If the degree of dominance can be experimentally determined, or the heterozygote recognised, and we can suppose that all forms mate together with equal freedom and fertility, and that there is no natural selection in respect of the allelomorphs, it should be possible to predict the proportions of the several components of the population with some accuracy. Conversely, departures from the calculated result would then throw no little light on the influence of disturbing factors, selection, and the like.

From the circumstance that dominance of either character is no essential accompaniment of allelomorphism, it must be determined whether the proportions of the two kinds of gametes produced by the heterozygote will vary with its individual character. Bearing on this question the experiments are very few. The determination from statistical study of zygotes must be exceedingly difficult, seeing that *both* resulting forms may be heterozygous. The ratio in which the heterozygotes are distributed in the second generation need not be the same as it was in the first, and unless this can be determined it will be almost impossible to get further with this particular inquiry.

Another difficulty will be found in the possibility that when the first cross-bred generation gives a mixture, the forms showing the usually recessive character (both in this and subsequent generations) may be *pure* recessives as regards their own gametes also (false hybrids of Millardet, see p. 61) though heterozygous in origin. To solve these difficulties before the gametes can be microscopically differentiated may be still impossible.

We have now simple and convincing explanations of many facts hitherto paradoxical.

1. *Heterozygous Forms.* It has long been known to breeders that certain forms cannot be fixed by selection indefinitely continued. In other words, when the most perfect examples of such forms are bred together, though they produce some offspring like themselves, they have also a large number which do not resemble them.

A case of this kind is seen in breeding crested canaries. The kind of crest desired for exhibition can, according to canary-fanciers, be

produced most easily by mating crested birds with non-crested, or plain-heads as they are called. If it be supposed that the crested character is usually dominant, we have a simple explanation. When crested birds are bred together a number of birds are produced whose crests are coarse and stand up, and others without crests. The latter are the recessives; the former we may suppose to be the pure *dominants. What the fancier wants* is a crest composed of long feathers lying evenly down over the head. These may be the heterozygotes, and consequently cannot breed true or be fixed by selection. Such birds bred together, give many plain-heads and birds with coarse crests. Fanciers hold that the plain-heads needed for crest-breeding should be themselves crest-bred, *i.e.* from families which have had crests among them. On the view here suggested this is probably a superstition, though one can easily see how it may have arisen[1].

If two crested birds are bred together it is advised that they should have imperfect crests, in all probability another form of the heterozygote[2].

Another case, to which our attention was called by Mr G. Thorne, of Broxbourne, is that of the Golden Duckwing Game Fowl. This colour can be produced by crossing Black-Reds with Silver Duckwing; but on attempting to breed the Golden Duckwing true, the colour breaks up again into its components[3].

Probably the impossibility of fixing certain colours in Pigeons also illustrates the same phenomenon.

Such forms have hitherto been regarded as exhibiting "instability." Of this instability there is now a satisfactory account.

A more complex instance of this may be the Andalusian fowl. The colour is a blue-grey mixed with dull black. The breed will not continue true to colour. Though a considerable proportion of Andalusians are produced, a number will be hatched which are too dark or too light in various ways and proportions. Selecting the best Andalusians effects nothing, and the constancy does not increase. There is, there-

[1] The fancier's view that the plain-head must be crest-bred is quite correct, because the heavy feathering (and perhaps skull-characters) are needed for a good crest. [Note from "corrigenda in Report I" published in Report II, 1905.]

[2] An account of these facts is given in Blakiston, Swaysland, and Wiener's *Canaries and Cage Birds*, p. 128. When birds with good crests are bred together the recessive "plain-head" is often produced, a fact which has been exaggerated by various writers into the statement that the offspring of cresteds are *always* plain-heads, or even always *bald*.

[3] See also Lewis Wright, *Book of Poultry*, 1886, pp. 289 and 356.

fore, a strong probability that the Andalusian is a heterozygote, though, doubtless, of a complex nature. Its gametes do not fully correspond to it, and its colour must be produced by a combination of dissimilar allelomorphs.

A point of great practical and theoretical importance would be the determination whether the increased vigour so commonly observed in the offspring of some crosses is or is not correlated with the union of dissimilar allelomorphs. Hitherto we have spoken of all the offspring of crossing as "crosses," alike. We must now recognise that when heterozygotes are bred together their offspring *may not be crosses at all*. The great vigour seen in the first cross is known not rarely to decline in the next generation bred from them, and it may be possible to see whether such vigour was in reality associated with the union of any recognisably dissimilar allelomorphs.

The existence of forms which are exclusively heterozygous leads to the contemplation of another possibility. In the heterozygotes we have spoken of, both sexes of course bear gametes transmitting each allelomorph. If, however, one allelomorph were alone produced by the male and the other by the female we should have a species consisting *only* of heterozygotes.

So long as the heterozygotes bred together, the offspring in such a case would come true, but a proof that they were heterozygotes would be obtained by crossing them with another species or variety. It would then be found that reciprocal crosses would not give the same result. That this is actually the case we know in certain instances, of which the most familiar amongst animals is perhaps that of the Mule (Mare × Jackass) and the Hinny (She-ass × Stallion)[1], and amongst plants the hybrids of *Digitalis*[2]. In most treatises on crossing other cases are referred to, and though probably many of them are based on experiments insufficiently repeated, there can be no doubt many are authentic. Gärtner[3] acutely observes that the phenomenon of dissimilarity between the results of reciprocal crosses is more likely to be found among diœcious forms.

2. *Selection and the Phenomenon of Dominance.* We have seen that the want of fixity in certain forms, though continually selected, may

[1] A good description of the differences between these forms is given by Cornevin, *Traité de Zootechnie*, 1891, p. 641.

[2] See Focke, *Pflanzen-Mischlinge*, 1881, p. 322; and Gärtner, *Bastarderzeugung*, 1849, p. 225. Other examples are given by Gärtner, *ibid.*; and by Swingle and Webber, *Year-book Dept. Agric.*, 1897, p. 401.

[3] *Loc. cit.*, p. 228.

at once be explained by the hypothesis that they are heterozygous only, and have no gametes corresponding to them. Another illustration of the failure of selection is the constant recurrence of a particular "rogue" in the best strains. Seed is never taken from such rogues. Every year they may be pulled up as soon as detected, but they continually appear.

The hypothesis that such a "rogue" is a recessive form *may* give a complete explanation of this phenomenon in many cases. Selection from *individuals* of known fertilisation would at once test the truth of this view, and might provide a means of producing a pure strain once and for all from the pure dominants.

It is well known that some of the best modern beardless wheats which have been raised of late years by crossing distinct varieties will give a small proportion of bearded plants. This is, of course, called "reversion" to a bearded ancestor used in the original cross.

From the experiments of Rimpau[1], we find that when bearded and beardless varieties are crossed, beardlessness is dominant, and the bearded character is recessive. By subsequent breeding a form is produced with a desirable character, and after a few years of selection it is found to give this character with sufficient purity and it is put on the market. It may be a bearded or a beardless form, but if the latter, the chances are that it will always produce a certain proportion of bearded plants[2]. This may happen in every case where there has been a *promiscuous* selection of many dominant plants, for any one of these may be a heterozygote and bear in each year both dominant and recessive germs.

The fact that the hornless breeds of goats still give some horned offspring is probably referable to the same cause. The point is of course not certain, but from the analogy of cattle (see p. 46) we may anticipate that the hornless form is dominant. In the polled breeds of cattle, which are never *promiscuously* selected, the polled character has naturally been easily fixed pure, but in goats selection among the *ewes* has been probably to a large extent promiscuous.

The phenomenon is without doubt occurring very widely in nature. To it we may perhaps attribute the undiminished persistence of some weakly varieties, which are unceasingly exterminated by natural or artificial selection without ever leaving offspring. Cases have only to be looked for to be found in abundance. We may note the paradox that, for anything we know to the contrary, a recessive allelomorph

[1] *Landw. Jahrb.* xx.

[2] Such a variety is Garton's Red King.

may even persist as a gamete *without the corresponding homozygote having ever reached maturity in the history of the species*[1]. It would be premature to trace out the deductions to which this suggestive fact points, but we see at once that it may give the true account of the phenomenon that domesticated forms constantly give rise to varieties not met with in the wild state, a fact often ascribed on insufficient grounds to the action of changed conditions in producing greater *variability*.

It will be clear—a point which may have some economic importance—that in any such case the recessive "rogue" can be eliminated by selection from *individual* plants or animals, breeding only from those which give no recessives on being self-fertilised, if hermaphrodite. If the organism be diœcious the process will be more elaborate, for it will be first necessary to test for recessive allelomorphs by fertilising with a recessive, and afterwards to fertilise those that gave no recessive offspring with a dominant similarly proved to be free from recessive influence. Nevertheless, it is certain that by this process alone can a strain of pure dominants be readily made.

"Purity" then acquires a new and more precise meaning. An organism resulting from an original cross is not necessarily pure when it has been raised by selection from parents similar in appearance for an indefinite number of generations. *It is only pure when it is compounded of gametes bearing identical allelomorphs, and such purity may occur in any individual raised from cross-bred organisms.*

An organism can be strictly defined as genetically pure if all its gametes when united with similar gametes reproduce the parent

[1] [In illustration of such a phenomenon we may perhaps venture to refer to the extraordinarily interesting evidence lately collected by Garrod regarding the rare condition known as "Alkaptonuria." In such persons the substance, alkapton, forms a regular constituent of the urine, giving it a deep brown colour which becomes black on exposure. The condition is exceedingly rare, and, though met with in several members of the same families, has only once been known to be directly transmitted from parent to offspring. Recently, however, Garrod has noticed that no fewer than five families containing alkaptonuric members, more than a quarter of the recorded cases, are the offspring of unions of *first cousins*. In only *two* other families is the parentage known, one of these being the case in which the father was alkaptonuric. In the other case the parents were *not* related. Now there may be other accounts possible, but we note that the mating of first cousins gives exactly the conditions most likely to enable a rare and usually recessive character to show itself. If the bearer of such a gamete mate with individuals not bearing it, the character would hardly ever be seen; but first cousins will frequently be bearers of *similar* gametes, which may in such unions meet each other, and thus lead to the manifestation of the peculiar recessive characters in the zygote. See A. E. Garrod, *Trans. Med. Chir. Soc.* 1899, p. 367, and *Lancet*, November 30, 1901.]

identically; and in practice the only way in which such purity can, by one breeding, be tested, is by crossing the organism in question with pure recessives.

There are also other classes of cases where progressive selection fails not only to fix a particular variety but to diminish the proportion of "rogues" beyond a fairly definite limit. We may first consider how far the principle of dominance may give an acceptable account of such cases.

In his most valuable book, *Die Mutationstheorie*, 1901, Professor de Vries devotes a chapter to the consideration of such phenomena, pointing out in a number of cases that progressive and continued selection has failed to fix a particular character. He draws the conclusion that such characters distinguish "half-races," as he calls them, which cannot be bred pure.

The cases taken are many-leaved clovers, a polypetalous Ranunculus, several plants with variegated foliage, and the biennial forms of certain species.

Selection in each case at first rapidly increases the proportions in which the selected form appears among the offspring, but soon a maximum effect is produced which is not surpassed.

Now in each of these examples fertilisation was left to insects, and though seed was saved from individual plants it is not in dispute that cross-fertilisation between them occurred. In Mendelian terms some might be pure *D*, some pure *R*, and some *DR*. Supposing dominance complete, eradication of the pure *R* forms annually does not extinguish them, for by the breeding of the *DR* forms *inter se* they will be continually reproduced.

There are no doubt many overlying complications in each of these cases, as, for instance, the probability that dominance is in these instances imperfect, but these will not change the main result.

The case of the biennial plants is especially interesting, as here we have strong indications that treatment and conditions may determine which character shall appear. For example, de Vries quotes the evidence of the Sugar Beet, a plant of great economic importance, to the breeding of which much attention has been devoted.

The plant which forms the large sugar-bearing axis is a biennial and does not flower until it has made the sugar-store. But from the best seed which has for generations been saved from such plants only, *there arises a small percentage of an annual form which runs to seed* without making a thick root at all. After years of selection the pro-

portion of such rogues is not diminished. Now, if it could be supposed that the annual is recessive and the biennial dominant, this is partly explained. On selection, seeds are taken from dominants only. But some of these will be pure dominants and others will be heterozygotes bearing *both* allelomorphs. The latter will each year give rise to a certain number of pure recessives, compounded of two recessive gametes. In the first years of selection, the proportion of recessives will be diminished rapidly by choosing seed from dominants only, but further *promiscuous* selection of dominants, unless continued for an indefinite time, will not altogether remove the recessives, for they arise from the dominants themselves[1].

But in these forms it is well known that several kinds of treatment, exposure of the young plants to frost, over crowding, heavy manuring, and forcing, will greatly increase the proportion of "runners." In the case of *Œnothera* de Vries has made some very convincing experiments, clearly proving this fact, and Rimpau has done the same for the Beet, showing that the number of "runners" can thus be greatly increased. There are then some which are biennial in any case, some which are biennial or annual according to treatment, and some which are in any case annual. This is strongly suggestive of the three Mendelian classes.

De Vries has also experimented by selection from the annual plants, getting of course a higher proportion of annuals. But it must be remembered that in order to prove that the annual character is recessive, and that it can, as such, be fixed by one selection, it is necessary to ascertain first that the plant chosen is not what de Vries calls a "facultative" annual—on this hypothesis, a *DR*—and secondly that it has not been cross-fertilised, particulars not yet forthcoming.

[1] It is of course only a conjecture that the biennial form is dominant in these cases, but, owing to the great importance of the subject, it seems worth while to call the attention of those interested to the possibility. Among the many investigations already made on the Beet it does not appear that the simple experiment has been tried of seeing if the annual or biennial form can be bred true from *individual* plants fertilised under proper precautions. Still less has the possibility of dominance been investigated. The only evidence known to us is that of Rimpau, that when the annual *Beta vulgaris* was grown near the cultivated form it bore two seeds which proved biennial and fifty-eight which were annuals. Rimpau conjectures that the two were crosses with the cultivated form, in which, as we should now say, the latter was dominant. But *B. patula*, an annual, emasculated and fertilised by cultivated Beets promiscuously, gave annuals only. Here there is a cross with another species, and the evidence is of doubtful application.

But even if the hypothesis of dominance could be successfully applied to these cases, there are others, at first sight similar, where it cannot be thus applied; for example, instances of varieties recessive in their differentiating character, producing annually a small but sensible number of a particular "sport," exhibiting a character already known to be dominant. Here we must suppose either that we meet the phenomenon of an *originating* variation—the "mutation" of de Vries: or possibly, which appears to be de Vries' view of half-races —the output of a certain number of such aberrant gametes is normally incidental to the development of the type-gametes. An objection to the latter deduction in some cases exists in the fact that the "sports" in question may be exceedingly rare, and therefore produced by few individuals only[1].

3. *Skipping a generation.* That marked individual peculiarities fail to appear in the immediate offspring, but may reappear in a subsequent generation, has been often observed, and the fact has taken a great hold on the popular imagination. It has not yet been shown that the distribution of any of these characters among the different generations in any line of descent is other than is to be expected on the hypothesis of pure chance. Nevertheless, we have now in the phenomenon of dominance a fact which may possibly be a real element in the causation of such appearances, and those who are familiar with statistics of inheritance, in man for example, might usefully study them with the possibility in view. The absence of the character in the first generation may indicate merely that it is recessive, and its reappearance in the next generation may be due to the heterozygote having bred with another individual also bearing the recessive allelomorph.

4. "*New*" *characters may be dominant.* We cannot as yet perceive any properties common to dominant as compared with recessive characters. It will be noted, however, that the view of many naturalists that the phylogenetically older character is prepotent, or, more correctly, dominant, is by no means of universal application. In poultry, for instance, both pea and rose combs are dominant against single, though the latter is almost certainly ancestral; the polydactyle foot is dominant against the normal, though a palpable sport. A point of some interest is that in both wheat and barley the beardless

[1] Excellent illustrations of this phenomenon in the case of high-class Peas have been lately supplied to us by Mr Arthur Sutton. Of these we hope to give details hereafter.

form is dominant, though we naturally, though perhaps incorrectly, regard it as a state normal in the one species, but an innovation in the other.

In cattle the polled form is dominant over the horned, though the former is a character which in our cattle has certainly arisen since domestication.

5. *Prepotency*. The conception of dominance avoids certain difficulties which are involved in the use of the term "prepotent." As we now know that the allelomorphs of the several characters may be quite independent, it is confusing to speak of the prepotency of an individual when all that we know is that one or more of its characters is dominant over the contrary character. Of the dominance or prepotency of the *whole* we know nothing. The diversity of the views which have been at various times expressed as to the respective powers of mother or father to confer special qualities has probably arisen from confusions thus caused. If the term prepotency is to be preserved it must be applied to characters rather than to organisms, and its use must be restricted to cases in which the character so qualified has been actually tested by combination with the contrary allelomorph in one heterozygote.

We have been accustomed to consider that a variety may be sometimes prepotent in respect of a given character and sometimes not prepotent. The whole evidence on which this view is based will in many cases now require careful verification, for, as was fully discussed in the case of poultry, such a result may really be due to an unsuspected heterozygote having been sometimes used for the other parent. The evidence, for instance, that on crossing pea comb and single comb the offspring may be sometimes pea and sometimes single would formerly have been thought a clear proof that pea comb was not always dominant, whereas it is now certain that much fuller evidence is needed to establish this proposition.

The existence of the so-called "false" hybrids of Millardet (see p. 61) is an even more serious difficulty besetting the conception of prepotency, for here, though the cross-breds are produced by a union of the male and female gametes of two varieties, it is quite uncertain that the characters of both parents are introduced at all.

As a rule fair uniformity prevails among the results of first crossings, and in every case in which a mixture of forms occurs the question must now be asked *whether the fact is not a proof that either or both of the parents are actually producing more than one sort of gametes.* It is,

no doubt, possible to conceive of the elements contributed by the two gametes respectively as engaged in a conflict so balanced that some supervening circumstances may give dominance to either side with varying frequency; but from what we now know of the nature of heredity, the conception of dissimilar gametes borne by one or both parents is just as easy to form, and no less probable on the facts.

6. *Sex.* It is often profitable to compare the phenomena of variation with those of sex, and if the suggestion alluded to in the last paragraph be found true, it is worth reflecting whether the determination of sex may not sometimes be a phenomenon similarly conditioned.

Note, added March, 1902

[There is already a considerable body of evidence in favour of the view that difference of sex is primarily a phenomenon of gametic differentiation. The evidence, however, seems to point to the conclusion that the differentiation is sometimes a phenomenon of the male cells and sometimes of the female cells, sometimes perhaps of both. Our attention has been called to a note by McClung[1], suggesting that the differentiation of the spermatozoa of many insects and of some other Arthropods, according as they do or do not contain the "accessory chromosome," may be an indication of differentiation in regard to sex. This body has been the subject of extensive study on the part especially of the American cytological investigators, and further researches regarding it may be a most profitable field of inquiry.

The fact that in *Nematus ribesii*[2], and in the Hive-bee, the unfertilised eggs produce males only, seems to prove that in those cases the female cells are carriers of the male character only, though whether there is sex-differentiation of the male cells is not yet known. On the other hand, we have more frequent cases of unfertilised eggs in other types producing females only.

But from the observations of de Buzareingues[3], it appeared that there is a more or less definite distribution of the sexes among the seeds of diœcious plants, the females being more commonly derived

[1] *Anat. Anz.* November, 1901, p. 220.

[2] Professor Miall has given me a reference to Cameron, *Phytoph. Hymenop.*, *Ray Soc. Monogr.* I, p. 26, where authorities are quoted. He tells me that the same result was obtained in experiments of his own.

[3] *Ann. Sci. Nat.* XVI, XXIV, and XXX, 1829, etc.

from seeds of one region, and the males from those of another. This of course is no proof of *original* differentiation of sex among the female cells, but it is readily consistent with that hypothesis.

On the other hand, as on the whole *against* the hypothesis that sex depends chiefly on gametic differentiation, may be mentioned observations—especially those of Wichura (*Bastardbefruchtung*, p. 44)—that the statistical distribution of sex among first crosses shows great departure from the normal proportions. The same has been seen by many hybridisers using animal types. But the further fact that there is a still greater variation in the statistical relations of the sexes in the *offspring* of hybrids, is rather favourable to the hypothesis.

The frequent occurrence of hermaphodites among *first* crosses is also difficult to explain on the present hypothesis.]

7. *Reversions.* With the Mendelian conception of the heterozygote as a form with its own special "*hybrid character*," we have a *rationale* of large numbers of "reversions"; for we already know many cases where heterozygotes do present the characters of putative ancestors. This fact reduces to harmony several groups of results where different experimenters, believing themselves to have worked with similar organisms, have reached seemingly contradictory conclusions. For some have used pure forms and others heterozygotes appearing in their guise.

The Nature of Allelomorphism

A. *Simple Allelomorphs*

The following list enumerates the principal cases in which the phenomenon of allelomorphism has either been actually proved to exist or may be safely inferred from the published records[1]. In each of these cases more or less definite dominance of one character has been found, and in this list the dominant character is put first:

1. Hairiness and absence of hairs (*Lychnis*).
2. Hoariness and absence of hairs (*Matthiola*).
3. Felted ears and smooth ears (Wheat)[2].
4. Prickliness and smoothness of fruits (*Datura*).

[1] [From the evidence of crosses kindly carried out for us by Mr Leonard Sutton we are able to add the "palm" leaf (palmatifid) and reddish stems of *Primula sinensis* as dominant characters, while the "fern" leaf (pinnatifid) and purely green stems are recessive characters.—March, 1902.]

[2] Rimpau, *Landw. Jahrb.* xx, 1891, p. 346.

5. Style long and short (*Œnothera*)[1].
6. Beardless and bearded ears (Wheat and Barley)[2].
7. Pointed seed and rounded seed (Maize)[3].
8. Round and wrinkled seed (*Pisum*).
9. Starch endosperm and sugar endosperm (Maize).
10. Inflated (generally hard) pods and constricted (generally soft) pods (*Pisum*, *Phaseolus*).
11. Axial distribution of flowers and terminal distribution of flowers (*Pisum*).
12. Tall habit and dwarf habit (*Pisum*, *Phaseolus*), to which, from experiments seen at Messrs Sutton's, we think we may safely add tall habit and dwarf procumbent habit (known to gardeners as "Cupids") in Sweet Peas (*Lathyrus odoratus*).
13. Entire petals and laciniated petals (*Chelidonium majus*)[4].
14. Normal zygomorphic form and peloric form (*Antirrhinum*[5] and probably *Linaria*)[6].
15. Normal habit and waltzing habit (connected with malformation of the aural labyrinth) (Mouse)[7].
16. Presence and absence of extra toe (Fowl)[8].
17. Pea comb and single comb (Fowl).
18. Rose comb and single comb (Fowl).
19. Polled and horned breeds (Cattle and doubtfully Goats)[9].

[1] De Vries.

[2] Rimpau, *loc. cit.* pp. 341 and 353. Since this paper was written we have received Tschermak's valuable analysis of the phenomena in regard to wheat, which considerably extends our knowledge of allelomorphism in that species (see *Ztsch. für d. Landw. Versuchswesen in Oester.* IV. 1901, p. 1029).

[3] Correns, *Biblioth. Bot.* LIII, 1901.

[4] De Vries.

[5] Darwin, *Animals and Plants*, ed. 2, II, p. 45.

[6] In the case of *Linaria*, Naudin found that on crossing a peloric *Linaria* with a normal one a mixture of normal and peloric plants resulted. As to the origin of the peloric parent there is no information, and consequently it may have been a heterozygote. See Naudin, *Nouv. Arch. du Mus.* 1865, I, p. 137.

[7] Von Guaita, *Ber. naturf. Ges.* X, 1898, p. 317, and XI, 1899, p. 131. For references to this interesting case we are indebted to Professor Correns.

[8] The allelomorphism is not yet fully proved in this case. It is the only obviously meristic character in which there is yet any evidence of allelomorphism.

[9] It is almost certain that absence and presence of horns are allelomorphic characters. In England there are three principal polled breeds of cattle—the Aberdeen-Angus, Galloway, and the Red Polled. The first two are black, the last red. Between these and the horned breeds crosses are annually made in large numbers. This is especially the case with the Angus, from which great numbers of cross-bred cattle are annually bred for the meat market. These are usually Angus-Shorthorn crosses, but other

20. White shanks and yellow shanks (Fowl).
21. White plumage and general brown coloration (Fowl)[1].
22. Several coloured forms of flowers and their white varieties.
23. Several colours of fruits and their xanthic varieties (*Atropa*, *Solanum*).
24. Several colours of seed coats.
25. Darker and lighter colours of endosperm (Maize).
26. Yellow and green cotyledons (*Pisum*).

With regard to seed colours, Correns has shown that the question is a complex one, depending on several factors. In Maize, especially, the seed skin and the several parts of the endosperm may all be independently concerned in giving the net result. Each must be considered separately, and in several cases the dominance is imperfect, and blendings may occur[2].

horned breeds are also occasionally used. The cross between a pure Angus and a pure Shorthorn is almost always a blue-grey without horns. Generally the horns are represented by loose corns of horny material, sometimes imbedded in the skin and not rarely hidden by the hair. Such "scurs," as they are called in the North, are objected to in the pure polled breeds and are mostly absent.

Notes of the cross-breds exhibited at the Smithfield Club Cattle Shows in 1888, 1889, 1898–1901 give the following results. The animals are classified according to the descriptions in the Catalogue. No doubt, however, the actual purity of the parent breed or breeds was in many cases doubtful. Taken as they stand, the numbers exhibited in these six years were as follows:

From {Polled Angus, Polled Galloway, Red Polled} × some horned breed, usually Shorthorn, and the reciprocal cross—104 polled, 13 horned.

From first cross animals bred as above, mated with a pure polled parent—23 polled, 1 horned.

From first cross animals mated with some horned parent—18 horned, 24 polled.

When allowance is made for the very rough materials out of which these figures come, it is clear that the facts cannot be very far from the Mendelian expectation. It is, however, likely that the allelomorphs concerned are not merely the horned character in its entirety, and total absence of horns. For in the offspring of (polled × horned) × polled, the horns, when they occur, are often *loose* though of fair size. If all parts were completely correlated we should expect *either* absence of horns (perhaps mere scurs) *or* ordinary horns like those of horned breeds. Probably, therefore, there is not *complete* correlation between the formation of horns and that of the bony cores which carry them, and these characters are divisible in transmission. Unfortunately the cross-breds are practically never bred together, so that the valuable evidence thus attainable is wanting. It should be mentioned that in offspring of (polled × horned) × horned the coat-colour character also breaks up.

[1] [White Dorking × Indian Game crosses are this year giving exceptions to dominance of white.—1902.]

[2] Full details given in Correns' memoir, *Biblioth. Bot.* 1901.

Between various simple allelomorphs correlations may of course occur. A few of these we know already. But in these cases of simple correlation the gametes may each transmit the correlated groups or the opposite allelomorph entire (see case of *Matthiola*, R. p. 81).

From the foregoing list it appears that allelomorphism may occur in a great diversity of characters, involving many different physiological factors.

In the plants albinism appears to be recessive, but in the case of fowls white plumage is dominant, though not completely so. It does not appear as yet that simple allelomorphism occurs between any two colours, of which neither is xanthic or albino.

B. *Compound Allelomorphs*

So far, in all or nearly all the cases we have considered, the dominant and recessive characters are each *simple*. In other words, when the heterozygotes breed together, they produce dominants and recessives like their parents, heterozygotes like themselves, and no other forms. The gametes therefore respectively bear characters which are the same as those of the varieties which were used to produce the heterozygotes. We have next to consider a numerous and important group of cases in which a character of one of the original parental varieties after crossing is itself split up. Of these we will give illustrations.

1. *Sweet Pea.* By the great courtesy of Messrs Sutton and Sons we have been permitted to watch many of the experiments conducted at their nurseries. We cannot sufficiently express our indebtedness for the splendid opportunities of study in these fields thus provided. For the most part, these phenomena are not dealt with in the present paper, and amongst many interesting results there witnessed we propose now to refer very briefly to the following only:

Sweet Pea (*Lathyrus odoratus*). Stanley, standard dark maroon or chocolate, with wings similar but somewhat tinged with violet, crossed with Giant White, gave *all* Giant Purple Invincible, *viz.*, standards as in Stanley, but wings blue. These first crosses self-fertilised gave Giant White, Giant Purple (without blue wings), Mars (a well-known red variety), Her Majesty (a full magenta, well known), and a form like Her Majesty, *but flaked with white*[1].

[1] It is possible that this complex result does not always occur; for in another case a Giant Rich Purple, very like Stanley, crossed with Giant White, gave seedlings *all* Giant Rich Purple. These on self-fertilisation gave a mixture of Giant White and Giant Rich Purple again. One plant of each on self-fertilisation gave only offspring like itself.

One plant of each was saved and its self-fertilised seed sown. Mars and Her Majesty came true. The Giant White was tested, and it came true also. The Her Majesty flaked with white, however, gave Whites, Her Majesty, and Her Majesty flaked white again. The Giant Purple gave Giant White, Her Majesty, Giant Purples, and two plants of a streaky cream colour.

The facts point to a higher degree of complexity than we can yet realise, but we see that the first crosses are all alike, though differing from the coloured parent. The same form, or something very like it, was often observed to come in other cases where a blue or purple parent was used in crossing. Now on self-fertilisation the first cross gave a variety of forms. It therefore produced a variety of gametes, not two kinds, but several. Of these forms some, Mars, Her Majesty (Giant White also in all probability), reproduced themselves exactly. Therefore they had only one kind of gamete, and they must be supposed to have been formed by the union of similar gametes. The purples, on the contrary, produced most of the whole series again, showing that they were producing a variety of gametes like the first cross parent itself.

Her Majesty flaked with white, gave some Her Majesty, some White, some Her Majesty flaked white. Therefore the flaked plants are heterozygotes, formed by the union of a Her Majesty gamete with a white gamete.

We are then led to the conclusion that the allelomorph transmitting the coloration of Stanley is *compound*, and that it can be broken up into simpler and possibly component elements. When *similar* elements, thus extracted, combine in fertilisation, they do not split up again on the formation of gametes. The constituents of the compound allelomorphs may perhaps be spoken of as *hypallelomorphs*.

The fact that Stanley did not occur again is another indication that its colour character had been broken up into *more than two* elements.

Another fact which may point in the same direction is that the purple formed on the first cross is different from that which recurs in the next generation. In fact, this Giant Purple Invincible results from the union of the whole compound allelomorph of Stanley with that of Giant White. We may suppose that it does not come again for the reason that the compound allelomorph has been broken up among the gametes borne by the first cross, and that the union of no two of these, or of any of them with white, results in that particular heterozygote form, Giant Purple Invincible. Inasmuch, however, as

Giant Purple Invincible, not yet distinguishable from that produced in this cross, is a well-known and stable form, there must *either* be gametes corresponding to it[1] (or its male and female gametes must be dissimilar and combine in that definite heterozygote, which is most unlikely). Till the experiment has been repeated on a large scale we must not lay much stress on the absence of Purple Invincible after the break up of the first cross, because in other experiments where White Cupid (a procumbent form) was crossed with Mme Carnot (a blue), Purple Invincible again resulted together with White Cupid (? the result of imperfect emasculation). These Purple Invincibles, self-fertilised, gave several forms, amongst them Mme Carnot and some Purple Invincibles again. Whether this indicates that the compound allelomorph is not wholly broken up, or that its character may again be synthetically reproduced, cannot yet be said. Corroborative evidence that the blue elements are definitely extracted from the "derived" Her Majesty was seen in the fact that this variety when crossed with various pink and cream kinds gives no blues or purples.

To the whole subject of the results of crossing Sweet Peas we hope to return when our own experiments are further advanced.

The probability is that in this, as in other similar cases of compound allelomorphs, there is a heterozygote form which may be common to several combinations of dissimilar gametes, and it is characteristic of such forms that they may reproduce *in appearance* some putative ancestor. It is to this class of phenomena that Darwin's famous "reversions on crossing" are probably to be referred.

2. *Poultry.* Another example of the splitting up of a compound allelomorph is probably to be seen in the poultry experiments. The first cross between Indian Game and White Leghorns, for instance, is white flecked with a few black or grey feathers, sometimes barred, sometimes irregularly marked with pigment. Such first crosses bred together give some dark birds and some light (see R. p. 108), the latter being sometimes pure white, sometimes flecked with black, and sometimes pile (brown and white). When White Dorkings are crossed with Brown Leghorns the result is very similar; but in each of these cases the dark birds resulting from the inter-breeding of the first crosses are not simply like their dark grandparent, but belong to several distinct

[1] Similarly from other crosses seen at Messrs Sutton's it is clear that the form called "Painted Lady" may be another heterozygote form, though the same is one of the oldest and most familiar fixed forms. According to Mr S. B. Dicks, there is good reason to believe the purple and the Painted Lady forms to be the oldest varieties. *Report of Sweet Pea Conference*, 1900.

types of coloration such as black, cuckoo, silver-grey[1], together with some more or less nearly reproducing the dark grandparental type. The numbers reared are far too small to justify a comprehensive deduction, but that the types of coloration thus produced have some definiteness is quite clear. Whether any of them will breed pure must be unknown till next season. As already stated, some of these colours are already well known as characterising various breeds.

Until experiments have been carried out with the express object of proving the compound nature of allelomorphic characters and of resolving them into their constituents, we can only gather indications of such phenomena from experiments undertaken for other objects. Of these there are a considerable number which leave little doubt that further examination would disclose such a result. We may mention the observations of von Guaita on mice, from which it appeared that the first cross of albino mice with black-and-white Japanese waltzing mice, gave a grey house mouse resembling in size, colour, and wildness the wild house mouse[2]. The first crosses bred together gave albinos, grey mice, black-and-white, grey-and-white, and black mice (with the waltzing character distributed among them in proportions closely obeying the Mendelian ratio); of these the albinos produced, with one exception, albinos only when bred together. The grey marked with white, bred together, produced no more blacks or black-and-whites; and the blacks and the black-and-whites bred together gave no more greys, though both descriptions may still give albinos. Facts like these strongly suggest that, with suitable mating, the classes could be shown to consist of the original albino, and a number of forms, some of which would henceforth be pure, while others would be found to be heterozygous.

3. Another case, possibly of the same nature, is that of the Himalayan rabbit, of which an account is given by Darwin[3].

The literature of pigeon fancying abounds with information pointing to a similar *rationale* of the colour phenomena there seen. Formerly

[1] The appearance of silver-grey in the offspring of first crosses between White Dorking and Brown Leghorn may be attributed to the certainty that White Dorkings were related to Silver-grey Dorkings. The colour may, nevertheless, have come from resolution of the Leghorn colour, for it is not peculiar to Dorkings, but is known in other breeds, *e.g.* Game Duckwings.

[2] Haacke, crossing albinos with grey-and-white Japanese waltzing mice, usually obtained the same results, viz. grey mice, but more rarely *black* mice. The latter result must be taken as indicating impurity in one or other parent. Vosseler, quoted by von Guaita, obtained greys only. See Haacke, *Biol. Ctbl.* xv, 1895, p. 45.

[3] *Animals and Plants*, I, p. 113.

the recipes given in such treatises as to the methods of mating to be followed for the production of particular colours would have seemed mere nostrums, but now we can see at least the general basis of fact whence they have been derived.

The experiments with stocks described (R. p. 81) give cases probably also analogous. Several forms crossed together all gave purple for the first cross, which on being self-fertilised gave other colours in addition to those of the pure parental forms and that of the first cross.

This conception of compound allelomorphs is almost the same as that which Mendel himself introduces in speaking of his *Phaseolus* crosses[1]. His analysis does not, however, seem to be strictly correct, and the subsequent reasoning is consequently obscure and not altogether valid. He says if the colour of the red *Phaseolus* be made up of $A_1 + A_2 + \ldots$, then on crossing with a white form a, hybrid unions are produced, $A_1a + A_2a$ + etc.

But it is the group $A_1A_2 \ldots$ which is allelomorphic to a, and the heterozygote is $A_1A_2 \ldots a$, and not $A_1a + A_2a$ + etc. It cannot be till the crosses form their gametes that the compound allelomorph breaks up.

It is not evident how this error of expression came about. Mendel in consequence misses the point that by the breaking-up of the compound character after the cross, new fixed forms may be produced by union of the elements of the original compound allelomorph, without any admixture from the variety with which the first cross was made. Such pure forms may be represented as A_1A_1, A_2A_2, etc. and of these we have already seen instances in the case of the Sweet Peas, Mars and Her Majesty.

Of the coloured forms appearing as offspring of the first crosses interbred, some are compounded of colour-bearing gametes meeting similar or dissimilar colour-bearing gametes, and some (like the Sweet Pea, Her Majesty, flaked with white) of a colour-bearing gamete meeting a white-bearing gamete.

We have good reason to believe that the compound allelomorph is not in every case resolved into its ultimate constituents when the gametes of the first cross are formed, and indeed we must suppose such imperfect resolution to be present whenever, as in the case of the Sweet Pea, among the resolved forms (White, Mars, Her Majesty) there occur complex heterozygotes like Giant Purple, which can itself produce a series of forms in the next generation. Such a form may be

[1] *Verh. naturf. Ver. Brünn*, 1865, vol. IV, p. 35.

represented as $A_2A_3 \ldots a$. It is to this class of complex heterozygotes that we conceive the Andalusian fowl to belong.

It is doubtful whether and in what sense we are entitled to regard the whole compound character as *one* allelomorph. Some justification for this conception is to be found in the fact that in the poultry crosses the light chicks bore to the *whole number* of dark chicks the proportions of 3 : 1. On the Mendelian hypothesis this must be taken to show that the cross-breds produce on an average white-bearing gametes equal in number to the whole number of colour-bearing gametes, which may bear the colour allelomorph in various stages of resolution.

By statistical investigation of such cases it should be possible to determine with some success how the unresolved characters are related to the elementary characters, and to make a scheme of *equivalence*.

It is, perhaps, hardly too much to suggest that in a great number of cases the familiar fact so often observed that first crosses bred together give a profusion of new forms may be capable of similar explanation. With such new forms the usual experience is that some breed true from the beginning, while some continue to give rise to other forms, of which some may have already been produced, while others again are new. The cases we have taken are those of colour-varieties, as the facts in those cases are clearer, but their nature is probably not different. It is in this sense that crossing may be truly spoken of as a "cause" of variability, and some picture of that phenomenon is now provided.

The importance of this reasoning lies in the fact that we can now recognise that these different new forms may be, in their genetic composition, diverse. We are no longer to expect that it is a matter of chance whether each will be able to transmit any of the other forms, but we perceive that this is a question to be determined by actual observation once for all. When such determinations shall have been made on a statistical basis we shall be able to state precisely the numerical proportions which the gametes of the several classes bear to each other, and hence to determine the actual number of constituents of the compound allelomorph and their relationships to each other. This investigation is now merely a matter for precise quantitative analysis.

Remembering that we have no warrant for regarding any hereditary character as depending on a material substance for its transmission, we may, with this proviso, compare a compound character with a double salt, such as an alum, from which one or other of the metals of

the base can be dissociated by suitable means, while the compound acid-radicle may be separated in its entirety, or again be decomposed into its several constituents. Though a crude metaphor, such an illustration may serve to explain the great simplification of the physiology of heredity to which the facts now point.

A marked feature in connection with compound allelomorphism[1] is the frequency with which in such cases one or more of the heterozygotes present what we have reason to regard as ancestral characters. To such "reversion" we referred in speaking of Sweet Pea crosses. The Sweet Peas produced a flower with purple standard and blue wings approaching what we may regard as a primitive Sweet Pea. Several white varieties of Stock produce a purple form; many of the crosses with the "half-hoary" type gave fully hoary heterozygotes. The Albino and Japanese mice produce a grey house mouse as their heterozygote. *Why* such heterozygotes should show ancestral characters we do not know; but we can now recognise that such "reversions" are heterozygous mixtures and not constant forms. To speak of such reappearances of ancestral characters as a reappearance of the ancestral *form* is entirely misleading. These heterozygotes will not breed true, and *are* ancestral in no real sense. Not only are they heterozygous and in constitution compound, but, as in the Sweet Pea, several different compounds agree in having the same ancestral form as their specific heterozygote.

It is unfortunate that Darwin's own experiments with poultry and pigeons were so complex that it is now impossible to disentangle the results or to use them for the purposes of these deductions. He records the most complicated unions of birds of different breeds, some homo- some hetero-zygotes, some exhibiting simple and others compound allelomorphs, and in the statement of results the all-important distinctions between the generations and the offspring of the several individual birds are often not observed.

To sum up the phenomena of compound allelomorphism, we may say that the evidence shows that the characters of a pure form when crossed with another may be broken up into component characters or hypallelomorphs, and that the decomposition may take place in various degrees of completeness.

To the variations which thus arise by resolution of compound

[1] There is no reason for supposing such reversion to be absent in all cases of heterozygotes formed by the union of *simple* allelomorphs, but the few clear cases know seem to be all cases including compound allelomorphs.

characters we propose to give the name *Analytical Variations*. There can be no doubt that a very large proportion of the discontinuous variations in colour, at all events, met with both in wild and domesticated species are of this nature. The fact that similar component forms are similarly related to each other and to the type, in various species, thus provides the true account of numerous phenomena of "parallel" variation.

The facts thus grouped suggest the following questions. Has a given organism a fixed number of unit-characters? Can we rightly conceive of the whole organism as composed of such unit-characters, or is there some residue—a basis—upon which the unit-characters are imposed? We know, of course, that we cannot isolate this residue from the unit-characters. We cannot conceive a pea, for example, that has no height, no colour, and so on; if all these were removed there would be no living organism left. But while we know that all these characters can be interchanged, we are bound to ask is there something not thus interchangeable? And if so, what is it? We are thus brought to face the further question of the bearing of the Mendelian facts on the nature of Species. The conception of Species, however we may formulate it, can hardly be supposed to attach to allelomorphic or analytical varieties. We may be driven to conceive "Species" as a phenomenon belonging to that "residue" spoken of above, hut on the other hand we get a clearer conception of the nature of sterility on crossing.

Though some degree of sterility on crossing is only one of the divers properties which may be associated with Specific difference, the relation of such sterility to Mendelian phenomena must be a subject for most careful inquiry. So far as we yet know, it seems to be an essential condition that in these cases the fertility of the cross-bred should be complete. We know no Mendelian cases in which fertility is impaired. We may, perhaps, take this as an indication that the sterility of certain crosses is merely an indication that *they cannot divide up the characters among their gametes*. If the parental characters, however dissimilar, can be split up, the gametes can be formed, and the inability to form gametes may mean that the process of resolution cannot be carried out. In harmony with this suggestion is the well-known experience of hybridisers, that if there is any degree of fertility in the first cross, with subsequent interbred generations the fertility may increase[1].

Such increase in fertility is generally associated with some greater

[1] Focke, *Pflanzen-Mischlinge*, p. 483; Gärtner, *Bastarderzeugung*, pp. 333 and 373.

approximation to one of the parental forms. In terms of our hypothesis, we may conceive this fact as denoting that offspring formed of gametes which have successfully resolved the characters of the heterozygote, and are not bearers of the irresoluble characters, can form their own gametes with less difficulty.

That the sterility of hybrids is generally connected in some way with inability to form germ cells correctly, especially those of the male, is fairly clear, and there is in some cases actual evidence that this deformity of the pollen grains of hybrids is due to irregularity or imperfection in the processes of division from which they result. It is a common observation that the grains of hybrid pollen are too large or too small, or imperfectly divided from each other[1]. Such conditions are what we should expect on the hypothesis here suggested[2].

However this may be, it would be of the utmost importance to discover at which of the divisions leading to the production of the gametes, the allelomorphic characters are divided. Correns has pointed out that the evidence of maize proves that in that case the two nuclei of the pollen tube must both be transmitters of the same character, for, in the fruit of the first cross between starch and sugar varieties, those seeds which have sugar endosperms produce pure recessive (sugar) offspring. This fact proves therefore that the nucleus which fertilises the embryo and that which fertilises the endosperm, are transmitters of the same character. Therefore, the separation of the characters does not take place in this case when the two generative nuclei divide from each other[3]. Further evidence on this question is

[1] See *e.g.* Naudin, *Nouv. Arch. du Mus.* 1865, I, p. 95, and Wichura, *Bastardbefruchtung im Pflanzenreich*, 1865, p. 37. Cases are easy to find.

[2] Remarkable observations bearing directly on this question have recently been published by Guyer (*Science*, XI, 1900, p. 248), as to the spermatogenesis in hybrid Pigeons. The species used are not named, and the account is very brief. He states that in both sterile and fertile hybrids much variation in cell-division was seen, inequalities in chromatin distribution were common and multi-polar spindles were abundant. In hybrid spermatogonia there were often more than eight (the normal number) large ring chromosomes. Sometimes there were sixteen small rings. In this case they usually located in two spindles, eight to each. Frequently both large and small rings were present. Guyer suggests, though apparently in ignorance of Mendel's work, that this phenomenon may indicate a "tendency in the chromatin of each parent species to retain its individuality." If so, he points out that in cells with two spindles and eight chromosomes, after division, some of the new cells will have chromatin from one parent and some from the other, and the observed "reversion" of the offspring of hybrids to parent species "may be due to the persistence of the chromatin of only one species in one or both of the germ cells."

[3] Correns inclines to the view (based on the fact that pollen grains of crosses be-

wholly wanting. Several attempts are being made by others and by ourselves to determine this point by crossing varieties with recognisably different pollens; but, so far, the desired mixture of dissimilar gametes in our cross-bred has not been satisfactorily observed. As soon as some means shall have been found of making visible that differentiation which we now know must exist between the germ cells of the same heterozygote, a vast field of research will be opened up. Till then, the microscopical appearances accompanying the segregation of the characters must remain unknown, and we are obliged to resort to the cumbrous and protracted method of deduction from the statistical study of the zygotes formed by the union of the several kinds of gametes.

Variation, especially discontinuous variation, of zygotes is in great measure thrown back on that of the gamete. We perceive, in fact, that the production of dissimilar gametes by one zygote may be compared, to take a rough illustration, to a bud-variation, constantly recurring in each heterozygote. Whether the divisions resulting in the formation of the dissimilar gametes are symmetrical or asymmetrical we cannot yet tell; but as in most cases of discontinuous variation, by sufficient searching, occasional instances, particular individuals or strains, will probably be found where the discontinuity is imperfect. As already pointed out also, the existence of exceptional gametes of a mosaic nature must already be inferred. It is unfortunate that so long as the statistical distribution of the zygotes is the only criterion by which the nature of the gametes can be deduced, even cases of impurity in extracted recessives—the readiest form in which imperfect differentiation will be seen—will not suffice to show whether there has been in fact such imperfect differentiation, or only defective dominance.

Mendel's discovery, it will be understood, applies only to the manner

tween forms of *Epilobium* differing in pollen colour do not show a mixture of the two parental colours) that the separation of characters does not take place when the pollen grains divide from each other, but when the generative nucleus separates from the vegetative nucleus. Such an observation is, however, surely inconclusive. The pollen grain is not the germ cell, but the carrier of the germ cell, and in any case there *may* be no universal correlation between the appearance of the pollen grain and the characters it transmits. From what we know of discontinuous variation, and especially from the analogy of that "dichotomy" of characters seen in various parts of hybrids, we incline to the view that the separation of characters will be found to occur at various divisions in various forms. Information on these phenomena is given especially by Naudin, *Nouv. Arch. Mus.* I, 1865, p. 150; Focke, *Oesterr. Bot. Ztschr.* 1868, p. 139; Macfarlane, *Trans. Roy. Soc. Edin.* 1895, XXXVII, p. 203.

of transmission of a character already existing. It makes no suggestion as to the manner in which such a character came into existence. The facts, however, leave no room for doubt that at least one character of each pair of simple allelomorphs has arisen discontinuously. The fact that the gametes of the cross transmit each member of the pair pure, is as strong an indication as can be desired of the discontinuity between them. From imperfection of the records, however, we cannot point to many cases where we know both that the origin was sudden, and that the characters obey Mendel's law, though no one practically acquainted with these subjects will feel any doubt that if those records were complete, there would be abundant evidence to this effect. A positive example, however, is that of *Chelidonium majus laciniatum*, of which the modern origin is recorded[1], and the allelomorphic nature was proved by de Vries[2]. It is scarcely doubtful that such varieties repeatedly arise. The Cupid Sweet Pea is another (p. 46).

With regard to the compound allelomorphs, it must be determined by further investigation whether they similarly can come into existence in their entirety, or whether they are capable of synthesis. At present, though we can perceive the fact that they are capable of decomposition, we know nothing of the reverse process.

In the cases we have discussed, it is plainly the simple allelomorph that has discontinuously arisen (cf. p. 42 above).

While we can hardly doubt that, of each pair of simple allelomorphs, *one* must have come suddenly into existence, we cannot tell whether this fact means that something is *added* to the original organism, or whether, from the first, the appearance of the new character is to be regarded as a *replacement* of the corresponding character. For example, we do not know whether the greenness of the peas is due to an *addition* of something to the whole sum of the yellow pea, or to a *substitution* of something for the yellow character. We may partly understand the physiological nature of the yellowness and the greenness, or to take a clearer case, of the relation of the starch endosperm to the sugar endosperm, but this is as yet no help in elucidating the question. If it shall appear that the process is one of addition, the conception of the characters *splitting* may prove an incorrect one, and some other metaphor must be substituted.

Of special importance in this regard will be the study of cases where

[1] For literature see Korschinsky, Heterogenesis, trans. "Flora," Ergänzungsheft, LXXXIX, 1901, p. 248.

[2] *Ber. Deut. Bot. Ges.* 1900, p. 87.

three or more characters are capable of mutual replacement. All cases studied so far are examples in which the allelomorphs are in *pairs*, but we know instances where three or more alternative forms of the organism occur, and an investigation of such cases may throw light on this part of the problem.

Attention of those who propose to experiment in this direction must, however, be called to the fact that so long as we are dealing with simple allelomorphs, though there may conceivably be more than two forms of gamete (apart from "mosaics," etc.), in respect of each group of simple allelomorphs, yet each zygote can, variation apart, bear two only. Consequently, no zygote can be formed by the sexual process which shall be capable of bearing more than two forms of gamete of each sex. But it is not inconceivable that by grafting or some other form of union, a combination of three or more allelomorphs in one organism may be brought about.

Non-Mendelian Cases. In the case of *Matthiola* and among the poultry, instances have been apparently found of definite departure from Mendel's law (R. pp. 81–6 and 107). It is certain that these exceptions at all events indicate the existence of other principles which we cannot yet formulate. But besides these cases there are three distinct classes of phenomena met with in breeding to which the Mendelian principles cannot be readily applied. It will be useful to consider briefly how each case departs from these principles, and whether by any modification they can be extended to such cases.

Such phenomena are:

1. The ordinary blended inheritance of continuous variations.
2. Cases in which the form resulting from the first cross breeds true.
3. The "false hybrids" of Millardet.

1. *Blended Inheritance.* At first sight it seems that cases of continuous variations, blending in their hereditary transmission, form a class apart from those to which Mendel's principles apply. But, though it may well be so, the question cannot be so easily disposed of. The essence of the Mendelian conception is, as we have seen, that each gamete may transmit one allelomorph pure. So long as each heterozygote can only exhibit *one* allelomorphic character, the dominant, we can from a study of the heterozygotes and their offspring demonstrate the purity of the gametes. But dominance is a distinct and subordinate phenomenon. We readily perceive that the heterozygotes may show either of the parental characters discontinuously, or various blends between them, while the gametes which composed the hetero-

zygotes may still be pure in respect of the parental characters. The degree of blending in the heterozygote has nothing to do with the purity of the gametes.

It must be recognised that in, for example, the stature of a civilised race of man, a typically continuous character, there must certainly be on any hypothesis more than one pair of possible allelomorphs. There may be many such pairs, but we have no certainty that the number of such pairs and consequently of the different kinds of gametes are altogether *unlimited* even in regard to stature. If there were even so few as, say, four or five pairs of possible allelomorphs, the various homo- and hetero-zygous combinations might, on seriation, give so near an approach to a continuous curve, that the purity of the elements would be unsuspected, and their detection practically impossible. Especially would this be the case in a character like stature, which is undoubtedly very sensitive to environmental accidents.

It is, of course, quite possible that the gametes in such cases do in fact vary as continuously as we see the zygotes do, but this cannot yet be affirmed. The great theoretical significance of this question should therefore lead us to suspend judgment for the present.

2. *First Crosses Breeding True.* With respect to this phenomenon no experiments on a large scale have yet been made. Most examples are recorded in the form that *A* and *B* were crossed together and produced a third form, *C*. The *C*'s were then bred together and some *C*'s were again produced. We hardly ever are told that in this generation *only C*'s were produced. Generally, however, we do not even know so much. The cases for example given by Darwin[1], are for the most part general statements that certain new and now definite forms, the Swede turnip, for instance, were produced by crossing. Any such case may, therefore, be merely one of the resolution of compound allelomorphs followed by selection of the forms produced by the union of similar component allelomorphs. This, indeed, is probably the true account of most permanent forms produced by crossing[2].

[1] *Animals and Plants*, ed. 2, II, pp. 73–77.

[2] We cannot avoid expressing a doubt whether the wonderful series of "mutations" which de Vries has lately recorded (*Die Mutationstheorie*, 1901) as arising from *Œnothera Lamarckiana* do not fall under suspicion that they may owe their origin to some unsuspected original cross. Nothing can take away the extraordinary interest which attaches to these experiments, but until it has been shown in the clearest way that the *Lamarckiana* which gave rise to the "mutants" is a genuine uncrossed form we must feel hesitation in accepting the conclusion which de Vries has drawn from the facts.

There remain, however, a few cases of which Mendel's[1] own crosses among *Hieracia* are a good example, in which a distinct form, produced by the first cross, has proved able to transmit its characters to its offspring. Of such cases we know very little. We may, perhaps, notice two features as apparently characteristic of these cases. First, that the results of the first cross may show no uniformity; secondly, that there is often a considerable degree of sterility.

In Correns' terminology such crosses are "homodynamous" and "homoögonous." De Vries speaks of them as *erbungleich*. In these instances the new form is able to give off gametes, male and female, carrying its own new character. Such facts plainly indicate a degree of complexity higher than that to which the Mendelian principles can apply, and for the present we have no insight into their nature.

3. *Millardet's "False Hybrids."* Some allusion must be made to the remarkable results described by Millardet[2], which have been the subject of frequent discussion among practical evolutionists. Put briefly, Millardet found that when certain varieties, especially of strawberry, are crossed together, (1) the cross-breds may precisely reproduce the maternal type, without any indication of the paternal characters; (2) in other cases the cross-bred individuals may show *either* the maternal characters pure (save in one case the colour of fruits) *or* the paternal characters pure. Seeds from plants thus exclusively reproducing one parental type themselves gave plants again exclusively of that type. To such forms he gives the name *faux hybrides* or *hybrides sans croisement*.

In order to estimate the significance of these facts we ought to know of what variations the pure forms are capable, when bred *inter se*, without crossing. Upon this point we have as yet no evidence. If we assume that each of the forms used would, if bred pure, transmit its characters regularly to its offspring, then we should have established that the heterozygote produced exclusively gametes, transmitting the character which appeared as "dominant" in itself, and a new order

This possibility is strengthened by the fact which Professor de Vries has told us, that the pollen of his *Lamarckiana* contains deformed grains, a point which is also mentioned by Pohl (*Oesterr. Bot. Ztschr.* 1895, XLV, p. 212) in a paper to which de Vries refers (*loc. cit.* p. 153).

On the other hand, we can scarcely suppose crossing to be the only cause determining the production of heterogeneous gametes, or in other words, variation in sexual descent.

[1] Mendel, *Verh. naturf. Ver. Brünn*, VIII, 1869. See also Swingle and Webber, *Year-book Dept. Agric.* 1897, p. 393.

[2] *Mém. Soc. Sci. Bordeaux*, sér. IV, 4, p. 347.

of facts is thus revealed. It is difficult to see any escape from this conclusion, but, on the other hand, if it could be shown that the pure-bred offspring of the one form could themselves exhibit the characters of the other parent used in the cross, we should recognise that the parent forms themselves produced mixed gametes, and in such a case we should expect that when similar gametes meet in fertilisation the offspring resulting would breed true. On the whole this explanation is very improbable, but as yet it is not wholly excluded in some of the cases in which Millardet's phenomenon is alleged to have occurred.

In our experiments with *Matthiola*, cases were described which, it can scarcely be doubted, are fully proven. The same is true of some of de Vries' instances[1], notably that of *Œnothera Lamarckiana* crossed with the *cruciata* var. of *biennis*. Possible instances occurred in regard to the combs of poultry (R. p. 122), though, as there pointed out, a simpler explanation is not altogether excluded in those examples. Such phenomena may perhaps be regarded as fulfilling the conception of Strasburger and Boveri, that fertilisation may consist of two distinct operations, the stimulus to development and the union of characters in the zygote.

Note, added March, 1902

[Several times in the course of these pages reference has been made to the phenomenon known as the "false hybridism" of Millardet. We are not aware that attempt has yet been made to elucidate that phenomenon. In view of the Mendelian discovery, we think it may not be altogether premature to suggest a possibility, which may perhaps be some guide to further experiment with this phenomenon.

In the false hybrid then, one or more characters are contributed to the zygote by one parent alone, to the exclusion of the corresponding character of the other parent. This exclusive character is exhibited on the development of the zygote; and that the opposite character is really excluded appears from the fact that the offspring of the "false hybrid" do not reproduce the excluded character.

The terms "false hybridism" and "false hybrid," though they have done good service, are clearly inconvenient for the fuller discussion that must arise respecting these facts, and we propose to denote the phenomenon by use of the term *monolepsis*, the ordinary result of fertilisation being distinguished as *amphilepsis*.

It is not yet certain whether monolepsis is a phenomenon peculiar

[1] *Ber. Deut. Bot. Ges.* XVIII, 1900, p. 441.

to recessive characters; but while we are fairly sure that some of the cases in which it is seen are instances of recessive characters, we know no certain example of the monoleptic transmission of a dominant character. By the nature of the case, positive evidence of such transmission must be peculiarly difficult to obtain; for the first cross-bred generation would have to be individually tested on a considerable scale by subsequent breeding before such a possibility could be established.

Let us first consider certain features of the process of fertilisation as it may be supposed to occur between gametes bearing similar allelomorphs—for example, an *R* character. Each gamete bears *R*, the zygote exhibits it, and the gametes produced by that zygote bear it again.

But we note that we do not *know* whether the character exhibited by such zygote is really the product of the allelomorph of *both* gametes, or is due to the exclusive development of that of one gamete only. Commonly we conceive of all characters of a zygote as the product of both gametes, and in cases of true blended inheritance we must so conceive them. Such a view also accords well with all that we know of the visible processes of fertilisation. Nevertheless, the fact is not certain in the case of the union of similar gametes, and the case may—to take a rough and partially incorrect illustration—be comparable to the known fact that the faculty of speech is, in the normal case, controlled by the centre in the left hemisphere only, the corresponding structures presumed to exist in the right hemisphere not developing or at least not becoming functional. We do not *know*, in fact, whether the character in the zygote depends on, or is in any way affected by, the fact that *both* gametes were bearers of that character.

But if we suppose that the zygote character is thus a product of the two similar allelomorphs in the normal case, we may on that hypothesis form a conception of what may be imagined to take place in the case of monolepsis. For returning to the heterozygote we perceive that on the formation of its gametes there is a resolution or separation of the two dissimilar allelomorphs which came into it at fertilisation. May we not then suppose that in the case of the homozygote a similar separation takes place? The gametes of the heterozygote *DR* are bearers of *D* and *R* respectively separated out of *DR*; may not the gametes of the homozygote, which are bearers of *R* and *R*, receive those allelomorphs by a similar separation occurring between *R* and *R*?

If this reasoning prove valid, we suggest the possibility that in the

case of false hybridisation the allelomorph is passed on from the zygote to the gamete without such resolution, and that thus it is not in a state which admits of its being affected by the contrary allelomorph of the other gamete. The case may perhaps be compared with the known fact that on separating the two segmentation spheres of an egg, each half may develop into a symmetrical larva.

Unproved as such a suggestion must necessarily be, it is in accord with several of the facts of crossing, of which no other account is as yet forthcoming. If, then, in a cross between D and R, an R be produced in circumstances which leave no doubt that such production is not due to mere environmental disturbance, we must suppose that the D character has never really *met* the R character.

Apart from examples of the appearance of a completely recessive form in the first cross, there are curious cases of the appearance of mosaic or pied forms in which the D and R characters form an irregular patchwork. In such a case Correns speaks of the characters as *pœcilodynamous*, a sufficiently expressive term. If, however, it were true that the pied condition is not really due to the dominance failing sometimes and succeeding sometimes, but to the existence in the mosaic of islands of the recessive character in the "paired" or unresolved state, we ought not to describe the phenomenon by reference to dominance at all.

In the introduction to this paper reference was made to the case of Canary—Goldfinch mules. Here the Goldfinch colour is normally dominant. It is said that, generally speaking, 99 per cent. of mules are thus "dark." As was also there stated, the belief is prevalent that in-breeding the hen Canaries has an effect in increasing the proportion of "light"—or canary-like mules. Others have disputed and denied the truth of this belief.

Nevertheless, it is generally admitted that to get "light" mules one should begin with a strain of Canaries which, on mating with the Goldfinch, throw some pied birds. On the hypothesis here suggested, the pied character is supposed to be due to the partially unresolved character of the recessive allelomorph. On in-breeding we may conceive the process of non-resolution on formation of gametes to be carried further. We have seen that cross-breeding leads to the fuller resolution of characters—in-breeding may lead to the contrary result.

With the Canary, as the mule is almost (if not quite) universally sterile, further experiment is impossible, but other cases are available for the experimental testing of this hypothesis.

If it is correct, it should appear that when on crossing a D and R a pied form is produced, showing patches of the R character, then such a pied form on crossing with the dominant again is more likely to give pied recessive or recessive offspring than a pure normal recessive would be, for we are on the hypothesis entitled to believe the gametes of the pied mule to partake of the same character as the zygote itself.

On the older view of breeding such a fact would be paradoxical; for the pied form, inasmuch as it already is part way to the D form, would be supposed *less* likely to show any R in its hybrid than the pure R form.

The fact that Tschermak in his crosses between the pea *Telephone* and yellow varieties obtained a considerable number of seeds greenish or patched with green, is consistent with this view; for this pea, though commonly a green or greenish pea, is liable to great variation, and is frequently mosaic or pied yellow and green[1].

The remarkable series of Orchid crosses given by Hurst[2], in which the female parent's characters alone appeared as the result of certain extreme crosses, seem rather to illustrate the possibility of parthenogenesis following the stimulus of fertilisation, without zygotic union.]

Galton's Law of Ancestral Heredity in relation to the new Facts

Such a preliminary survey of the phenomena of heredity as we have attempted would be incomplete without some reference to this subject. We note at once that the Mendelian conception of heredity effected by *pure* gametes representing definite allelomorphs is quite irreconcilable with Galton's conception in which *every* ancestor is brought to account in reckoning the probable constitution of every descendant. With respect of each allelomorphic pair of characters we now see that only four kinds of zygotes can exist, the pure forms of each character, and the two reciprocal heterozygotes. On Galton's view the number of kinds is indefinite.

At first sight it may appear that as the two views are quite incompatible, they must relate to different classes of phenomena. In so far as Galton's law relates to continuous variations with blended inheritance, this may be the case (see p. 59); but in some of the cases following Galton's rule, notably that of the colour of Basset hounds,

[1] See Weldon, *Biometrika*, I, 1902, Pt. 2.

[2] *Journ. Roy. Hort. Soc.* XXIV, 1900, pp. 104–5.

the colours dealt with are discontinuous[1]. Let us consider what evidence there is in this case that the gametes are not pure tricolour *or* non-tricolour, as we should now expect them to be. The first question is, does either colour show dominance? If either were dominant it must clearly be the tricolour, and in view of the fact that both tricolour × tricolour and non-tricolour × non-tricolour are said to have given mixtures, neither colour can be supposed to be exclusively dominant. In this case, therefore, as it is impossible to tell which individuals are pure and which are heterozygotes, Galton's results might possibly have occurred, *and the gametes yet be pure*. More cannot be said without reference to the actual details out of which the tables were constructed.

Attention may also be called to the fact that in cases which fully obey Mendel's ratio (and exhibit dominance), two of the commonest matings happen to give the same result as they would do on Galton's expectation, though the latter is founded on wholly different considerations. Mendel, for instance, expects

$$DR \times DR \text{ to give } 3\ D\text{'s and } 1\ R,$$

and that $DR \times R$ will give equal numbers of D's and R's. Both these results are, *cæteris paribus*, to be expected on Galton's law, so that it might need a good deal of experiment to distinguish the two classes of cases. A clear distinction would, however, at once be found by comparing the result of $DR \times R$ with that of $DR \times D$.

Bearing this in mind, and having regard to the considerations mentioned in the paragraph on blended inheritance, it is impossible to avoid the suggestion that Galton's law may be a representation of particular groups of cases which are in fact Mendelian, in the sense, that is, that there may be purity of gametes in respect of allelomorphic characters. In any case it is now certain that Galton's law cannot be accepted as "universally applicable to bi-sexual descent."

By any practical breeder this must have been always expected, for he knows that while he can rapidly fix some characters, some never come true at all, and others will not come true with any certainty after long selection. The expectation after simple selection is, in fact,

[1] Pearson (*Roy. Soc. Proc.* LXVI, 1900, p. 142) has suggested a distinct formula for these cases of alternative inheritance, which he terms the "Law of Reversion." He urges that such phenomena should be treated separately from those of blended inheritance. Both laws alike are of course based on the numerical composition of the ancestry.

quite different for different characters. Mendel's principle disposes of a great part of these difficulties, for we now know that any recessive character may be fixed at once by selecting recessives, and that this fixity may have nothing to do with the novelty of the character, its "prepotency," etc., and that the heterozygote may never come true.

Galton's law in fact does not recognise that *absolute* purity which is so common a phenomenon in breeding, as it is in nature. The breeder, in hosts of instances, is not, as a matter of fact, constantly troubled by recurrences of forms with which, even in his own practice, his strain has been crossed. Of this the full explanation is now seen; for if two similar gametes meet, their offspring will be no more likely to show the other allelomorph than if no cross had ever taken place.

Conclusion

We have now sketched the principal deductions already attained by the study of cross-breeding, and we have pointed out some of the results now attainable by that method. The lines on which such experiments can be profitably undertaken are now clear and a wide field of research is open.

The properties of each character in each organism have, as regards heredity and variation, to be separately investigated, and, for the present, generalisation in regard to those properties must be foregone. The outlook, in fact, is not very different from that which opened in chemistry when definiteness began to be perceived in the laws of chemical combination. It is reasonable to infer that a science of Stoechiometry will now be created for living things, a science which shall provide an analysis, and an exact determination of their constituents. The units with which that science must deal, we may speak of, for the present, as character-units, the sensible manifestations of physiological units of as yet unknown nature. As the chemist studies the properties of each chemical substance, so must the properties of organisms be studied and their composition determined.

To the solution of the practical problems of heredity, and a determination of the laws of breeding both plants and animals, this is the first step. The attainment of these solutions is now only a question of time and patience.

That the same method will give the key to the nature of specific differences, we may perhaps fairly hope. Certain it is that until the

several characters are thus disentangled and their variations classified, no real progress with this question can be expected[1].

[1] It is absolutely necessary that in work of this description some uniform notation of generations should be adopted. Great confusion is created by the use of merely descriptive terms, such as "first generation," "second generation of hybrids," etc., and it is clear that even to the understanding of the comparatively simple cases with which Mendel dealt, the want of some such system has led to difficulty. In the present paper we have followed the usual modes of expression, but in future we propose to use a system of notation modelled on that used by Galton in *Hereditary Genius*. We suggest as a convenient designation for the parental generation the letter P. In crossing, the P generation are the pure forms. The offspring of the first cross are the first filial generation F. Subsequent filial generations may be denoted by F_2, F_3, etc. Similarly, starting from any subject-individual, P_2 is the grandparental, P_3 the great-grand-parental generation, and so on. We suggest this terminology here for the consideration of others who are working in the same field. All that is essential is to obtain uniformity, and it is quite likely that a better system may be suggested.

NOTE ON THE RESOLUTION OF COMPOUND CHARACTERS BY CROSS-BREEDING

[*Proceedings of the Cambridge Philosophical Society*, XII, 1902]

IN the recently-published part of his *Mutationstheorie* (Lief. IV. pp. 194–206), Professor de Vries records evidence of a valuable kind respecting certain cases of resolution of compound characters, and offers an interpretation of the phenomena. On consideration it seems doubtful whether this interpretation is not unnecessarily complicated, and it is the object of the present note to suggest a simpler account.

It will be remembered that in a case of simple Mendelian inheritance the offspring of heterozygotes, AB, self-fertilised or bred *inter se*, consist of only three forms, viz. the two homozygous forms AA and BB, representing the pure parental types, and one heterozygous form AB repeating that of the first cross. In such a case we recognise that this result is due to the fact that the gametes of AB are each bearers of either the A or the B character in its entirety. In the constitution of these gametes the characters A and B are alternative or *allelomorphic* to each other.

But already many examples are known in which when two pure forms A and B are crossed, the gametes of the AB's are bearers not simply of characters A and B, but of a number of new characters formed, as we may conceive it, by the resolution of the compound character of one (perhaps both) of the original pure forms. Until lately we had no evidence as to the statistical relations of the several gametes in such a case of resolution. By the work of de Vries and of Tschermak[1] we are provided with some materials for calculating these relations. From the distribution of characters among the offspring in these cases, and from the statistical relations of the several zygotic forms to each other, it is clear that the resolution and redistribution of characters may take place in several different methods, but until the facts of the next generation (grandchildren of the hybrid) shall have been more fully studied, we can scarcely appreciate the relation of these methods to each other. In one instance, however, that of de Vries' *Antirrhinum*, the evidence as to this generation (F_3

[1] Tschermak, "Ueber die gesetzmässige Gestaltungsweise der Mischlinge," *Ztschr. landw. Versuchswesen in Oesterr.* 1902, Tab. II–V.

of my notation) is more complete, and we can attempt to realise what has taken place in that case.

In most of the instances hitherto studied the compound character is a colour-character[1], which is resolved after a cross with a white variety, and such an example is that of de Vries' *Antirrhinum*, which I propose to consider here. In this case a red *Antirrhinum* was crossed with a white, giving a first cross (generation F_1) red like the red parent, white being recessive. F_1 on self-fertilisation gave a somewhat miscellaneous offspring (generation F_2), which could nevertheless be classified with fair accuracy into four forms, which de Vries calls Red, Flesh colour, Delila[2], White. These four forms existed in numbers approaching the ratio 9 : 3 : 3 : 1, if the minor differences are neglected.

This ratio 9 : 3 : 3 : 1 suggests to de Vries that there is here a phenomenon of "Di-hybridisation," a term used to denote the case of a cross between parents differing in *two* pairs of allelomorphic characters, as, for example, between a *yellow round* pea and a *green wrinkled* pea. In this latter case, if we call the heterozygote (F_1) $YRGW$, then, as we know, the offspring of self-fertilisation will be in appearance

$$9\ YR : 3\ GR : 3\ YW : 1\ GW,$$

and in reality

The 9 $YR = 1\ YRYR + 2\ YRYW + 2\ YRGR + 4\ YRGW$
The 3 $GR = 1\ GRGR + 2\ GRGW$
The 3 $YW = 1\ YWYW + 2\ YWGW$
The 1 $GW = 1\ GWGW$.

In interpreting his case of resolution on the analogy of di-hybridisation, de Vries regards the red parent as consisting of a union of flesh colour, F, and Delila, D, corresponding to the two dominant characters, yellow and round, while he conceives the white parent as representing the *two* recessive characters, which he calls W and W', though it is not suggested that W differs from W'.

The first cross he represents as

$$\begin{array}{c} \text{White} \times \text{Red} \\ W + W' \times F + D \end{array}$$

giving $W + W' + F + D$, the red hybrid.

[1] Indications however are not wanting that similar phenomena of resolution may occur in regard to structural characters also.

[2] Pale tube with red lips.

The offspring of self-fertilisation he represents as

1 FD	appearing	Red
1 FW'	,,	Flesh colour
1 WD	,,	Delila
1 WW'	,,	White
2 $FD + FW'$	,,	Red
2 $WD + WW'$	,,	Delila
2 $FD + WD$	,,	Red
2 $FW' + WW'$	,,	Flesh colour
4 $FD + FW' + WD + WW'$	,,	Red.

It was found by experiment moreover that $F \times D$ gives the red again. Other experiments showed that one of the D plants produced only D, and one of the F plants produced only F offspring; that other D plants might give a mixture of D plants and white plants; and that other F plants might give a mixture of F plants and white plants. Finally some red plants gave reds and F plants, while others gave reds and D plants.

In de Vries' account it seems to me that great complication is introduced by the attempt to express the *unresolved* red as $F + D$; and the representation of white by $W + W'$ is still more open to objection, for here at least there can be no reason to suppose *two* characters concerned. In fact the white is only represented as $W + W'$ because it is *crossed* with a compound character.

These difficulties, and others to which they lead, do not yet seem inevitable, and one is tempted to look for a simple account. Assuming the distribution of offspring to follow the ratio 9 R : 3 F : 3 D : 1 W, this result would equally be arrived at on the hypothesis that the hybrid of red × white, $R \times W$, produced *equal numbers of gametes of each sex having the characters R, F, D, W, respectively.* The fortuitous union of these would give 9 R : 3 F : 3 D : 1 W as before. The actual composition of the offspring would be as follows:

The 9 $R = 1\,RR + 2\,RF + 2\,RD + 2\,RW + 2\,FD$
The 3 $F = 1\,FF + 2\,FW$
The 3 $D = 1\,DD + 2\,DW$
The 1 $W = 1\,WW$.

We know from the experiments that R is dominant to both F and D; that F and D are each dominant to W; and that $F \times D$ gives R.

On this hypothesis the serious theoretical difficulties inherent in the other view are avoided. Far more than a mere question of

notation is involved. On de Vries' view the gametes must have the four forms *FD, FW′, WD, WW′*, so that the white character would be present in three out of the four gametes, though in differing capacities. From the records of the results thus far there seems no good reason for introducing these difficulties, or for regarding the case as one of di-hybridisation.

In attempting to apply either hypothesis to de Vries' other cases or to Tschermak's results in *Phaseolus*, various complications are encountered, and it is clear that in those phenomena other processes are concerned. Until there is a fuller experimental basis discussion of these cases is scarcely possible. To this subject I hope to return when the experiments on resolution of characters undertaken by Miss Saunders and myself are further advanced. Nevertheless, while our conceptions of allelomorphic characters, simple and compound, are in process of formation, it seemed desirable to point out how an unnecessary complication might be avoided.

From all that we know of these cases of resolution it seems fairly certain that the *whole* of a compound character need not be resolved on the first cross, but that the cross-bred may bear some gametes which transmit it in its entirety.

The visible phenomena of cell-division would suggest that the number of gametes bearing the simple character of one parent—here the white—should equal the *sum* of those representing the other parent and bearing the compound character and its various components. On the view here suggested, the number of gametes bearing the simple character is regarded as equal to the number of *only one* of these classes; and in the case under discussion the latter so far seems the more acceptable account.

We must, however, remember that in this case the *simple* character is *recessive*, the compound being dominant; and we naturally inquire if when a *dominant simple* character is crossed with a *recessive compound* character, the result would be the same. Whether the fact has a relation to this matter of dominance or not cannot be said, but in the only case I can adduce of a cross of the latter kind, namely that of a white and a coloured breed of poultry, there seems to be reason for the belief that the white gametes are as numerous as those of the various coloured ones collectively, for in the latter case the ratio 3 light to 1 dark (in generation F_2) seems distinctly indicated as the result of breeding the hybrids *inter se*.

In conclusion, since the resolution of a compound character may

be spoken of as an *analysis* leading to a distribution of the components among the gametes, the term *synthesis* should surely be reserved for a recombination that has taken place in such a way that the *gametes* become bearers of the compound character again, as they were in the pure compound form. In the place referred to, de Vries, however, using "analysis" as above, speaks of the union of *F* and *D* gametes to form a red *zygote* as a "synthesis." But until we know in some given case that the zygote so produced breeds true, and forms gametes bearing the synthesised character, the term synthesis seems inappropriate. If we use "analysis" for a distribution of component characters among gametes, "synthesis" should be reserved for a reconstitution of the compound character in the gametes.

In a sense, of course, the union of the gametes in the zygote leads to an apparent synthesis—$F \times D$, for instance, giving a zygote resembling the original *R*—but to use the term in that sense introduces great obscurity. Further difficulties would arise also from the fact that we already know cases where *various* pairs of dissimilar gametes lead to the formation of the *same* heterozygote form which may exactly reproduce the compound character of a pure type. Clearly there is no true synthesis here; for while the pure type could be resolved into its several components, each heterozygote would contain only the elements brought in by the particular gametes which produced it.

ON MENDELIAN HEREDITY OF THREE CHARACTERS ALLELOMORPHIC TO EACH OTHER

[*Proceedings of the Cambridge Philosophical Society*, XII, 1903]

THE object of this note was to call attention to various possibilities attainable by a modification of the Mendelian method. In the ordinary method the constitution of the gametes in the first cross (F_1) is tested by breeding such individuals *inter se* or with a pure recessive. The ensuing generation (F_2) will consist of a mixture of dominant and recessive individuals; but if the proportions depart from the expected 3 : 1 or 1 : 1, it is not possible to tell whether such departure is due to change in relative numbers of dominant and recessive gametes, to imperfect segregation of characters, or to change in dominance. This question can in part be answered by a method which consists in crossing F_1 produced from a parent having one dominant character, with another heterozygous individual having a different dominant character (the same recessive being used in both cases). In the poultry experiments described, rose comb (R) and pea comb (P) were used as the two dominants, single comb (S) being the recessive. When RS was crossed with PS, F_2 showed the four expected forms RS, PS, SS, and RP, each well characterised. The RP combs have a highly peculiar structure, resembling the "walnut" comb of some Malay fowls, the comb almost always being *feathered to some extent*, and generally crossed by a curious band of small feathers.

In F_3, RS gave rise to only R and S birds. No doubt the PS would give only P and S, and the S birds, S only. But if R and P had been completely segregated in F_1 the RP birds should be incapable of producing any singles in F_3. In the experiments $RP \times RP$ did give some singles, and therefore, assuming that S is not a hypallelomorph of R or P (which is being tested), a proof is provided that the segregation of R (or perhaps P) from S may be imperfect. That it may also be perfect for other R and P gametes has of course been previously established in several cases by breeding from dominants in F_2, some proving homozygous dominants, while others were heterozygotes. The ratios in which the several sorts of gametes are produced by the "walnut" birds have not been clearly made out. Complications arise from the fact that the segregation of R from P may be imperfect, for

some "walnuts" occur in F_3 from walnut × single. At present it seems likely that *R*, *P*, *RP*, and *S* are produced in equal numbers, but various experiments are needed to settle the point. A note of these qualitative results seemed of value as indicating possible lines of work, which if pursued on several subjects may considerably extend our knowledge of gametic differentiation.

Possibly the *F* and *D* forms raised by de Vries from *Antirrhinum* (*Mutationsth.* II, pp. 197 and 353) are somewhat analogous examples of imperfect segregation. An indication might be got by breeding from the reds formed by extracted *F* × extracted *D*. If whites then occur we should have proof that *F* was one hypallelomorph + white, and *D* another hypallelomorph + white, and the problem would be greatly simplified.

THE PRESENT STATE OF KNOWLEDGE OF COLOUR-HEREDITY IN MICE AND RATS

[*Proceedings of the Zoological Society of London*, II, 1903]

WITH the revival of interest in the experimental study of variation and heredity which has followed the discovery of Mendel's work, Mice have naturally been chosen by several investigators as a subject for experiment. To the breeder mice offer attractions from their small size, cheapness, healthiness, and rapid rate of multiplication. They have further the great advantage that the same male can be simultaneously tested with several females. They are, however, short-lived, one and a half years being a high limit of the breeding age. There are also more serious drawbacks. They are extremely addicted to eating their young. It is not easy to label a live mouse in a permanent fashion, and special methods have to be adopted for tracing the identity of the individuals, which in such work is indispensable. Another difficulty arises from the fact that mice present few readily estimable features of structure. Also, though there are now many types of colour, few of them as yet exist as pure strains, and hence it is not easy to obtain reliable material with which to begin the experiments. Nevertheless, in spite of these drawbacks, the subject is a good one, and there can be no doubt that our knowledge of heredity can be rapidly extended by experiments on mice. As regards Rats the case is similar, save in one respect, in which there is a very remarkable difference, namely that the colour-types of fancy rats are as yet extremely few. For this reason, though the scope of experiment is reduced in the case of rats, some serious complications are eliminated, and certain fundamental questions, as, for example, the relation of pied to self-coloured varieties, could probably be studied more easily in rats than in mice.

As a great deal of work on these species is now being done, it has seemed to me useful to codify the chief information already at our disposal, and to state as carefully as is yet possible some of the more immediate problems presented by the existing facts.

It would greatly assist discussion of these problems if uniform names could be used for the colour-types. An attempt is therefore made to suggest such names, and to indicate how the types may be recognised. The specimens examined for this purpose have been

obtained chiefly from Mr J. Wilton Steer, of 45 Raleigh Road Hornsey, N., and from Mr Atlee, of Royston, Cambs., and I am greatly indebted to both of these well-known breeders of mice for information and assistance. The microscopical examination and discrimination of the types was carried out by Miss F. M. Durham. This work is only in a preliminary stage and, it is hoped, will form the subject of a separate communication.

Microscopical examination shows the hairs of mice to contain numerous minute medullary spaces separated from each other by bridges of keratin. These spaces are arranged in longitudinal rows, the number of which varies from one to four (perhaps five), thick hairs having usually more rows than thin hairs. The pigment is deposited in two ways: (1) massed in the proximal walls of the medullary spaces, and (2) scattered in the external cortex. Since air bubbles out of the spaces when reagents are applied, the spaces probably open to the exterior.

The pigments in wild *M. musculus* or *sylvaticus* are readily seen to be of three kinds: (1) Densely opaque *black*. (2) Less opaque *brown*. (3) Transparent *yellow*. The chemical nature of these pigments and their possible relations to each other seem to be quite obscure. If the hairs are cleared of air, the three kinds of pigment can be recognised. On treating with 40 per cent. aqueous solution of potash, the yellow dissolves at once. The brown disappears much more slowly, but is rather more soluble than the black, which can withstand the treatment more than 24 hours, though ultimately it also (and the keratin) disappears.

The brown may be present in both medulla and cortex; the black is chiefly deposited in the medulla, but may be cortical also, while it is doubtful whether the yellow is ever present except in the medulla.

All these pigments may coexist in the same hair; but hairs are found with only black and brown, others containing only black and yellow. Other types possibly occur. The lighter colour is mostly peripheral (in hairs which contain other colours), but brown often is present in the cortex at levels where the medulla contains black.

In *M. sylvaticus* the condition is similar, but the amount of black is less.

The different colour-types of fancy mice are due to the presence or absence of one or more of these pigments in various amounts. Both the yellow and the brown may exist separately, without any other

pigment being discoverable, but, so far, no mouse has been seen having *black* only, some brown being always associated with black.

Each chief type of coloration, black, brown, and yellow, exists in at least two forms—the one more *intense*, the other more *dilute*. The dilution, which affects both medulla and cortex, seems to be due to greater scarcity of the pigment-granules, not to diminution in their size.

The following list includes all the types examined, though some probably remain to be seen. Waltzing mice, so far, have not been examined. The fanciers' names are generally retained, as on the whole distinctive and practical. Owing, however, to the ambiguity in the use of the term "fawn" to denote both "yellow" and colorations containing other pigments, the term "yellow" is used for the type containing yellow pigment only.

1. *Ordinary Golden* (or *Agouti*). The colour of *M. musculus*, having same *three* pigments. Exists in at least two strains, one rather darker than the other. This is doubtless the "grey" of most writers. Pied forms and strains common.

2. *Cinnamon Agouti*. Like (1) but yellower. Contains *brown* and *yellow*, without black.

3. *Sable*. This rather striking type is like (1) on the back, but with yellow hairs interspersed at sides. Flanks almost wholly yellow. Pied with white this colour gives the so-called "tricolor."

4. *Blue-and-tan*. Not examined microscopically. [Probably sable in which black is diluted.]

5. *Chocolate* = *Plum*. Contains brown alone. May be pied.

6. *Silver-fawn*. A diluted form of (5). Many hairs have colourless tips.

7. *Yellow*. Contains yellow only. Often called "fawn," though this term is also applied sometimes to colour containing brown or black. When dark pigment is present in association with predominant yellow the colour is spoken of as "dingy" or "sooty fawn."

8. *Cream*. Diluted yellow.

9. *Black*. Both black and brown present, without yellow. The bases of the hairs are the darkest, and the black does not extend to the tips of the large contour hairs, which are brown. Hairs behind the ears or on belly are a still lighter brown. Complication arises from the fact that at least two kinds of black exist, known as "black" and "sable-bred black," viz. thrown by sables. These two kinds probably differ in their heredity-properties. Pied forms common.

10. *Blue.* Diluted form of (9); both black and brown pigments coexisting. Blues may be thrown by the "blacks" (not sable-bred) and then breed true. Pied forms exist.

11. *Albino.* No pigment in any part. As albinos, however produced, breed true to the albino character generally, if not universally, individuals of dissimilar origins are often mixed together. One strain at least, that of Mr Atlee, is recognised in the fancy as having special features of size and shape, and has been kept distinct for many generations.

12. *Black-eyed white.* Strains of this type have been independently produced twice, perhaps oftener. The degree of pigmentation in the eye varies in at least one strain, some eyes being full black, others looking blackish red. Whether the type ever breeds quite true we cannot say. In our experience offspring with small black marks occur (compare phenomenon seen in albino Guinea-pig, p. 81).

13. *Variegated.* In these, irregular *small* spots of black or chocolate occur on a white ground. Such forms are quite distinct from the ordinary piebald and Dutch-marked (viz. like the Dutch rabbit) combinations of colour with white.

In comparing colours care must be taken that specimens are of similar age and in similar moult-stages. Differences of intensity of colour are of course characteristic of different strains, and probably intermediates can be found; but there is no doubt of the practical distinctness of each of the forms enumerated. "Brindling," viz. lighter or even white hairs distributed as ticking, occurs in some of the coloured varieties, as in rabbits, but we have not been able to examine specimens.

As to the age and mode of origin of the several forms little is known certainly. Several conditions are plainly due to resolution of compound characters, such as often follows crossing in animals and plants. The blue, the black-eyed white, and the variegated are certainly productions of the last few years; the rest (? sable) have existed for a long time.

The question how far *M. sylvaticus* has been used in the production of the varieties is a very important one. The experiment was suggested many years ago in *Fancy Mice* and has probably been often tried. Mr Atlee has given me a most circumstantial account of a cross with this species made by him nine years ago on black-and-white does, and I feel no reasonable doubt that it was actually made. The first generation were "agoutis" of very large size. Later generations gave

amongst others a strain of blue, and of black-eyed white. A strain of agouti has also been saved from it. He tells me that this formerly had the *white feet*, a character he carefully bred out. Such a cross may have affected the whole race of fancy mice at the present day. Our search for structural characters referable to *sylvaticus*, however, has failed to show any case of *one* pair of pectoral mammæ (as in *sylvaticus*) or any case of *long* hind foot. All specimens examined were pure *musculus* in these features. On the other hand, a feature sometimes seen in fancy mice, and greatly valued by exhibitors, is a *large eye*, much exceeding the size in an ordinary *musculus*. But this eye, though large, is still smaller than that of *sylvaticus*. Nevertheless the large eye is a modern feature in the fancy, and I think it not impossible it may have been derived from a *sylvaticus* ancestor. Further experiment alone can decide this question.

In order to appreciate what follows, the reader must have some acquaintance with at least the outline of the Mendelian principles of heredity. In this simplest expression these principles, as they are exhibited for instance in the experiments of Cuénot (12), are easily comprehended; but when we pass from these simplest phenomena to the more complex facts elsewhere witnessed, we soon reach difficulties which our experimental evidence is as yet only adequate to elucidate tentatively and in part.

Cuénot experimented by making reciprocal crosses between albino, pink-eyed, fancy mice, and wild grey mice (*M. musculus*). He was careful to use *wild* mice in order to be sure that his coloured form was pure. As a result he obtained always and without exception grey mice. In Mendelian terms, grey is therefore *dominant* over albinism, which is called by contrast *recessive*. The first filial generation thus produced, which we may conveniently call F_1, when bred *inter se*, gave a total of 198 greys and 72 albinos, constituting the second filial generation, or F_2. The ratio of dominants (D) to recessives (R) is here 2·75 to 1, a fairly near approach to the ratio 3 : 1, which on the simplest form of the Mendelian hypothesis is to be expected. In other words, the facts are, as Cuénot stated[1], in agreement with the supposition that in the formation of the gametes of the hybrid F_1, there is complete segregation of the grey colour from albinism, and that in both male and female hybrids there are on an average equal numbers of gametes produced bearing each of these two characters.

[1] Cuénot's paper seems to be the earliest application of Mendelian principles to animals.

According to the same hypothesis, the grey mice in F_2 should consist of pure or *homozygous* greys (DD) and of *heterozygous* greys (DR) in the proportion of 1 : 2.

Cuénot tested this to some extent by breeding the F_2 dominants *inter se*, and found that some pairs gave the expected mixture, while others gave dominants only. Qualitatively therefore the result is the normal one. It is not stated that the "extracted" albinos were tested, but there is little doubt that, in accordance with *almost* universal experience, they would have produced nothing but albinos.

A leading fact illustrated by Cuénot's experiments, viz. the recessive nature of albinism, is borne out by the whole series of experiments under review. The fact is true of albinos in mice, rats, guinea-pigs[1] (Cumberland (13); Castle (7)), and rabbits (Castle), so far as experiments have reached. Cases of the production of albinos by coloured rabbits (*e.g.* Polish by Dutch, albinos by silver-greys) are frequent in the fancier's literature. The contrary, the production of coloured animals by albinos, is not, so far as I know, illustrated by a single case, with the following exception. In the later editions of *Fancy Mice* (Upcott Gill), Dr Carter Blake, formerly secretary of the Anthropological Institute, commenting on the statement that albino mice of whatever parentage produce nothing but albinos, writes (p. 16) that a pair of albinos produced some brown-and-white, some plum, some grey, and some albinos. If this result occurred under all precautions, it stands alone.

Nevertheless, we should be cautious in declaring the result impossible, for in Mendelian experiments the observer must be on the look out for the appearance of a character, elsewhere a definite dominant, *as the consequence of crossing two dissimilar recessives*. Not only may a dominant colour be produced by crossing two forms having a recessive colour—*e.g.* purple flowers by crossing the white *Datura lævis* with white *D. ferox*; purple flowers in Sweet Pea by crossing white "Emily Henderson" round-pollened form with the long-pollened form of the very same white variety; purple flowers in the Stock by crossing two white varieties:—but also a dominant *structural* character, hoariness, may be produced by crossing glabrous (recessive) stocks of different colours, *e.g.* red and cream, or red and white[2]. In

[1] Small "smudges" are said to occur irregularly in albino cavies, however pure.

[2] This statement is based on results of experiments made by Miss E. R. Saunders, as yet unpublished.

each of these cases the appearance of an atavistic character occurs as a consequence of the union of gametes bearing dissimilar characters; but the character in which the reversion appears is of a class different from that in which the parental differentiation was seen.

The same may very possibly be true of animals also. But in each of the cases known, the two varieties united, though alike bearing the same recessive character, differ obviously in some other respect; and we know that the cross-bred raised by their union is a heterozygote, *i.e.* a zygote formed by the union of dissimilar gametes. It is, I think, scarcely likely that Carter Blake's case of the mice is really to be so regarded, and on the whole the hypothesis of error is more probable; but the possibility that colour may be influenced by structure, and structure by colour, must be remembered.

Naturally we may inquire whether albinism in Man is not a similar recessive. Castle has given evidence pointing in this direction. The occurrence of albinism in the families of first cousins (see Day, Seligmann, etc.) is consistent with this view; but there are a few recorded cases of the occurrence of albinos in the offspring of albinos breeding with normal parents, where the hypothesis that the normal parent was *DR* is not at all easily admissible. No case of the union of two human albinos is known to me. The matter cannot here be further discussed, and the reader must refer to the literature, the most important paper being that of Cornaz[1].

There are a few cases on record where the production of albino offspring by animals and plants must almost certainly be regarded as the occurrence of a new and original variation, though the cause of such sporting is entirely unknown.

We here encounter the first problem calling for experimental study. What *is* an albino? We know that it appears to form no pigment; but such a body has other characteristics also. While the blood of pigmented animals shows intravascular clotting on the injection of nucleo-proteids, that of the albino is declared to be unaffected. The mountain hare is said in this respect to behave as a normal in its summer coat, but as an albino after the winter change. How these differences are related to the want of pigment we do not know. Such an inquiry offers a wide field for experiment. In particular, we ought to know how the albino or the normal behaves towards the nucle-

[1] The student of albinism who refers to the paper of Legrain (*Bull. Ac. M. Bruxelles*, IX, 1866) should remember that it is the curious instance cited by Darwin (*Life and Letters*, I, p. 106) as a deliberate invention.

proteids of an *albino*, and so forth. However this may be, there seems to be but little doubt that the albino-bearing gametes can generally segregate that character entire, as they divide from the colour-bearing gametes of the hybrid zygote of any colour; and if we knew more clearly what is the real physiological difference between colour-secreting and albino organisms, we might get a clearer conception of the nature of such segregation.

We may consider next the work of Crampe, which is on a large scale and relates entirely to Rats. His latest paper is dated 1885 (10), and consequently is pre-Mendelian in treatment. He bred nearly 14,000 rats, and made elaborate records and tables of conclusions. Many of these observations are readily available so far as they provide simply qualitative as opposed to quantitative evidence; but after many attempts I have not succeeded in unravelling the material enough to group the statistics in Mendelian form[1]. Though only a sketch can be here given, many of these qualitative observations are of great value and will provide a basis for future work.

In rats the Mendelian rules, in their simplest form, are plainly inadequate to express the facts, and we soon meet a number of deductions of specific application, each needing full investigation. Crampe's account is long and difficult to follow. At first sight also it seems not wholly consistent in certain particulars, but the conclusions here summarised seem well established.

Breeding albino rats with wild *M. decumanus*, Crampe found that F_1 might have *one of two forms*, being either a self-grey like the wild type, *or* grey with white marks. Unfortunately, no precise description of this and of the other broken-coloured rats is given, and we do not know the precise extent and distribution of the white[2]. According as F_1 presented the first or second form, the subsequent offspring produced from F_1 bred *inter se*, differed. The whole series of colours presented by such offspring is arranged by Crampe in seven types, thus:

1. Self-grey.
2. Grey with white marks.
3. White and grey.
4. White (albino).
5. Black-and-white.
6. Black with white marks.
7. Black without marks.

[1] The figures given, (10) pp. 555 and 612, are the likeliest, but even these obviously contain certain heterogeneous elements now not distinguishable with confidence.

[2] First crosses shown me by Miss Douglas were grey except for an irregular but small amount of white on the chest and belly. I take this to be Crampe's type 2.

The self-coloured grey in F_1 gave in their posterity all the typ *except* 3 *and* 5, but F_1 of type 2 gave all seven types.

The nature and cause of the heterogeneity in F_1 is as yet u explained. Such an occurrence is, however, not rare. In my ow poultry experiments, for example, the dark feathers scattered in tl white F_1 raised between a brown and a white breed may be eith chequered or plain black. According as one or the other form appea in F_1 the posterity probably differ, though this point is not y established in the case of poultry.

The existence of two classes in F_1 indicates in all probability tl existence of two classes of gametes, either in the wild *decumanus* in the albinos, but in which we cannot say. From the evidence, seems that both forms of F_1 could be produced by the same pair parents, but I cannot find the fact explicitly stated. Both forn occurred in F_1 not only when *decumanus* was crossed with albino, bı also when it was crossed with type 3 and with type 5.

Only the albino could cause all seven types to appear in progen (F_2, etc.) raised from a cross with the wild type.

The albino was recessive to all the other six types, and albinos whatever parentage gave nothing but albinos when bred *inter se*. Th point was elaborately tested. Crampe states that albinos true-bre for some generations behaved differently from extracted albinos, tl former being, as he says, merely "absorbed," *i.e.* recessive, on crossir with colour; while extracted albinos gave, as I understand him, mixture of ancestral forms when they were crossed with other type This part of his paper ((10) pp. 573–5) is difficult to follow; and cannot find any example showing precisely the nature of the distin tion he means to emphasise so far as *albinos* are concerned. We mu here await fresh experiments. We readily see, however, that thou in respect of its albinism we may regard the albino as always tl same, it may obviously be retaining other characters derived fro various progenitors. Accordingly we find, as will appear, albin apparently of the same species manifesting different properties crossing. I suspect, however, that Crampe is here extending to tl albino a generalisation really based on a mistake arising from mi conception respecting the phenomenon of dominance. [See no added p. 105.]

We may now, though the evidence is imperfect, consider tl significance of the appearance of these many new forms in F_2. Th phenomenon is a most usual result of a cross between distinct varietie

It is the source of the majority of our new garden varieties, and of many at all events of the *colour*-varieties of domestic animals. In general terms we can declare that the result of the cross—the "asymmetrical fertilisation," to speak strictly—is the production of a diversity of gametes. Pending histological research, we cannot tell the origin of the characters borne by these gametes; but from many circumstances it seems inevitable that they must be regarded as created in such a case partly by *resolution* of the character brought in by the dominant—which we therefore call a *compound* character, and partly by the imperfect segregation of that compound or of its components from the recessive character (and its components if it be also resoluble). In most cases the process of resolution is not complete for *all* the gametes; and some of the gametes are bearers of the wholly or partly unresolved character, just as *all* the colour-bearing gametes were in Cuénot's simpler case. The Mendelian hypothesis leads us to believe that the actual numbers of each type of gamete will be on the average definite, and that the union of any two of them will give rise to a zygote of definite character.

The number of types of gametes and their several properties can only be determined on a minute analysis of each member of the series of zygotes by exhaustive breeding. No such evidence is yet complete in any one case, but we see already in certain cases that some of the F_2 are homo- and some hetero-zygous, and we are beginning to suspect the ratios of the gametic forms in a few simple cases.

Returning to Crampe's evidence, though the ratios are quite uncertain, we find that the several types had different properties.

On breeding specimens of each type *inter se* he found the following behaviour:

Type	1	might give types		1	2	–	4	–	6	7
,,	2	,,	,,	1	2	3	4	5	6	7
,,	3	,,	,,	–	–	3	4	5	–	–
,,	4	,,	,,	–	–	–	4	–	–	–
,,	5	,,	,,	–	–	–	4	5	–	–
,,	6	,,	,,	–	–	–	4	5	6	7
,,	7	,,	,,	–	–	–	4	–	6	7

In other words, each type is dominant to albino and the wild type is dominant to all. The grey forms are dominant to the black. The black-and-white of type 5 is recessive to type 6 (black with white markings), but the self-coloured black does not contain type 5. These

are some of the deductions from the table. The peculiarities of types 3 and 5 are especially noteworthy and call for fresh experimental study.

It appears that types 3 and 5 could be ultimately bred true. As to 6 and 7 the evidence is not very clear; but as I understand the account, neither was completely freed from throwing the other. The breeding in these types was the least successful and extensive. Possibly they are illustrations of the *Mittel-rassen* of de Vries. It is especially noteworthy that the grey-and-white type 3 and the black-and-white type 5 do not give rise to self-grey gametes or to self-black gametes, a fact found again in mice. We see therefore that there are gametes for black-and-white and for grey-and-white, each of which may behave as a single character and dominate over albino.

Similarly when pure black-and-white was crossed with the wild species, all the coloured types might appear in F_2 but no albinos ((10) pp. 555–6). Therefore, in this very important case, when black-and-white of type 5 appeared in the posterity of such a cross, they were *all* homozygotes and produced only their own type (p. 555). This fact may furnish a useful basis for a new experiment. In strict accordance with our expectation, Crampe found that black-and-whites which gave albinos when bred *inter se*, gave albinos if crossed with albinos; but when they did not produce them themselves, they did not when bred with albinos.

The similar variety, grey-and-white (type 3), is always homozygous except when it appears as a dominant containing types 4 or 5. But if I rightly understand Crampe's use of the word "*constant*," type 5 is not produced by crossing type 3 with the wild form, unless it was already brought in as recessive to type 3. On the other hand, type 3 can be produced (in F_2) by crossing type 5 with the wild form. It is most desirable that the properties of these two types (3 and 5) should be fully explored. They give a chance of investigating the resolving powers of a recessive that is not albino, and free from several complications attending the use of the latter.

When we try to picture what is taking place in the resolution effected by types 3 and 5, Crampe's figures, though too imperfect and irregular to justify a positive statement, show pretty clearly that these particular recessives do not appear nearly so often as 1 in 4; and consequently it is *primâ facie* likely that some of the new types of gametes are formed by imperfect segregation, and are combinations containing elements of both the dominant and the recessive—a

phenomenon indicated by experiments with other forms of animals and plants (cf. de Vries' resolution of *Antirrhinum*).

These are some of the chief deductions apparent from Crampe's work. Many others will strike a careful reader and are indeed given by the author, but for these reference must be made to the original.

From the want of details the important question of the identity of the several types is not easy to settle, but I think that we may allot Crampe's varieties among the well-known types of rats, with fair confidence, as follows:

1. The wild *decumanus*.

2. Like *decumanus*, but with a more or less sharply defined white area on the ventral surface (together perhaps with white on the feet).

3. Head and shoulders wild colour, forming the "*hood*" of the fanciers. This is continued in a broad *stripe* down the middle of the back to a *patch* on the rump. The rest of the body is white. The coloured area may be considerably extended on to the flanks, and more rarely[1] the dorsal stripe may be broken.

4. Albino.

5. Like 3, but black being substituted for wild colour.

6. Like 2, but black instead of wild colour. This type is known in the fancy as the "Irish" variety.

7. Self-coloured black.

With respect to the kinds of pigments in rats I have as yet no information. The distinction between black and the wild colour is apparently less sharp than in mice, and hoth black and black-and-white rats have a good deal of dark brown hair, especially in the edges of the black patches of the parti-coloured, and on the belly of the self-coloured black.

No doubt there is also some change with age, moulting, etc.[2]

Crampe ((9) p. 393) mentions the black stripe in his black-and-whites, and there is practically no doubt that his var. 3 and var. 5 are correctly referred to the hooded and striped types. He remarks that by selecting those with stripes so wide that the rats were more black than white, he got no nearer to breeding blacks. Similarly whites

[1] This is Miss Douglas' experience. In this respect strains doubtless differ, for Mr F. Swann tells me he formerly kept a strain in which the stripe was generally broken.

[2] Crampe records ((9) p. 395) changes with age in piebalds from "grey" to black and *vice versâ*, both colours appearing together in the transition. The change in the direction of darkening seems to be normal as the adult fur grows. In the same place he mentions a rat as "*Gelb-grau.*"

could not be bred from the whitest grey-and-whites. The types are in fact definite, and cannot be built up by cumulative selection.

I am indebted to Miss Douglas for much information as to the varieties of rats and for the loan of specimens. She tells me that rats coloured otherwise than the varieties named are exceedingly rare. Irregularly piebald or spotted rats occasionally occur, but she has tried recently to obtain such rats from fanciers without success. In her experience the type 6 breeds true or nearly so. Of the blacks examined by me this type had less of the brown hair than type 7.

A striking feature appears from the rat-evidence, namely the absence of yellow, blue, chocolate, and indeed most of the varieties so familiar in fancy mice. On superficial examination, the colour of a wild rat is not very greatly different from that of a wild mouse. In rabbits also the yellow as well as the black forms are common. Yellows or yellow-and-whites are also familiar in guinea-pigs, fowls (buff, and "pile"), and pigeons. Miss Douglas has heard of a pair of cream-coloured rats, but otherwise I can find no records of any kind of yellow in the fancy. As blacks are so easily produced by resolution in the rat, the absence of the corresponding yellow and chocolate is remarkable. One is tempted to inquire whether the existence of black gametes does not suggest that yellow or at least chocolate gametes must also exist. The problem of their disappearance raises many important questions as to selective union between gametes, and others too elaborate to develop now. As there are no yellows, so also there are no chocolates.

Another noteworthy fact is the complete absence of blue rats. This particular stage in the diminution of the amount of dark pigment is well known in mice, rabbits, cats, and several birds, but it is unknown in rats. There is of course no question that such forms would have been preserved if they had been seen by fanciers. Either yellow or blue rats would be worth several pounds. We may take it therefore that these particular resolutions, or perhaps mutations, cannot be produced by any of the means by which they have been produced in other forms. Conceivably, if some distinct species were crossed with our fancy rats, some of these forms might be created. Similarly there are no "Himalayan" rats, *i.e.* pink-eyed with patches of colour (blackish or yellow), forms well known in rabbits, guinea-pigs, and in the "Japanese" waltzing mice.

To sum up the evidence as to rats, we have clear proof of the segregation of certain types of gamete—the albino, the black-and-white,

and the grey-and-white, though the ratios in which they are produced by heterozygotes are not yet determined. Further, there is proof that certain of the colour-types exhibit definite valency (*Werthigkeit* of Tschermak) and dominate over each other according to a regular system. Of the other colour-types one, viz. type 2, is almost certainly a definite heterozygote form, and is probably incapable of being made into a pure race.

We may next consider the further evidence regarding mice. By the great kindness of Mr F. G. Parsons, I am permitted to include in this paper notes of 50 matings made by Mr Parsons in conjunction with Dr S. M. Copeman. These experiments were made with other objects in view and are still in progress, but as they stand they are a valuable contribution to the question of the inheritance of colour. The notes which Mr Parsons has placed at my disposal are here given exactly as they were received. I have merely inserted the letters *DR* and *DD* according as the results show that the individual in question was a heterozygote containing albino, or that it was free from the albino character. Those not thus distinguished cannot be discriminated by the existing evidence.

The following abbreviations are used: *bl.*, black; *br.*, brown = chocolate; *blw.*, pied-black; *brw.*, pied-brown; *w.*, albino.

Experiments made by Mr F. G. Parsons

	Mating		*Offspring*		
(1)	*w.* ♀ *A*	× *blw.* ♂ a (*DR*)	1 *blw.*	—	3 *w.*
(2)	,,	× *w.* ♂ β	—	—	7 *w.*
(3)	,,	× *brw.* ♂ (*B* × a) (*DR*)	—	1 *brw.*	3 *w.*
(4)	*w.* ♀ *B*	× *blw.* ♂ a (*DR*)	2 *blw.*	1 *brw.*	4 *w.*
(5)	,,	× *w.* ♂ β	—	—	5 *w.*
(6)	,,	× *brw.* ♂ γ (*B* × a) (*DR*)	—	—	5 *w.*
(7)	,,	× ,,	—	4 *brw.*	1 *w.*
(8)	*blw.* ♀ *C* (? *DD*)	× *blw.* ♂ a (*DR*)	3 *blw.*	1 *brw.*	— (1 eaten?)
(9)	,,	× *w.* ♂ β	2 *blw.*	1 *brw.*	—
(10)	*w.* ♀ *D*	× *blw.* ♂ a (*DR*)	2 *bl.*	1 *br.*	1 *w.*
(11)	,,	× *w.* ♂ β	—	—	5 *w.* (1 eaten?)
(12)	,,	× *brw.* ♂ γ (*B* × a) (*DR*)	—	2 *br.*	6 *w.*
(13)	,,	× ,,	2 *bl.*	2 *br.*	4 *w.*
(14)	,,	× *blw.* ♂ a (*DR*)	3 *bl.*	1 *br.*	2 *w.*
(15)	*w.* ♀ *E*	× *blw.* ♂ a (*DR*)	2 *blw.*	2 *brw.*	4 *w.*
(16)	*w.* ♀ *F*	× *blw.* ♂ a (*DR*)	1 *blw.*	1 *brw.*	2 *w.* (5 eaten?)
(17)	,,	× *w.* ♂ β	—	—	7 *w.*
(18)	*w.* ♀ B^1 (*B* × a)	× *blw.* ♂ a (*DR*)	2 *blw.*	—	3 *w.* (2 eaten)
(19)	*w.* ♀ B^2 (*B* × a)	× ,,	2 *blw.*	—	1 *w.* (3 eaten)
(20)	,,	× *w.* ♂ ε	—	—	8 *w.*
(21)	*w.* ♀ B^3 (*B* × a)	× *blw.* ♂ a (*DR*)	4 *blw.*	—	3 *w.* (1 eaten?)
(22)	,,	× *w.* ♂ ε	—	—	9 *w.*
(23)	,,	× *blw.* $C^{3\cdot 1}$ (C^3 × a) (*DR*)	5 *blw.*	—	2 *w.*
(24)	*blw.* ♀ C^1 (*C* × a) (? *DD*)	× *blw.* ♂ a (*DR*)	7 *blw.*	—	—
(25)	,,	× *w.* ♂ ε	2 *bl.* 4 *blw.*	—	— (1 eaten?)

	Mating		Offspring
(26)	*brw.* ♀ $C^2 (C \times a) (DR)$	$\times$ *blw.* ♂ $a (DR)$	— 1 *brw.* 1 *w.*
(27)	,,	$\times$,,	2 *blw.* 2 *brw.* 2 *w.* (3 eaten)
(28)	,,	$\times$ *w.* ♂ ϵ	1 *blw.* 4 *brw.* 1 *w.*
(29)	,,	$\times$ *brw.* ♂ $C^{2\cdot 2} (DD)$	— 7 *brw.* —
(30)	,,	$\times$,,	— 6 *brw.* —
(31)	,,	$\times$,,	— 7 *brw.* —
(32)	*bl.* ♀ $D^1 (D \times a) (DR)$	$\times$ *blw.* ♂ $a (DR)$	5 *bl.* — 2 *w.*
(33)	,,	$\times$ *blw.* ♂ $C^{2\cdot 1} (DR) (C^2 \times a)$	7 *bl.* 1 *blw.* —
(34)	*bl.* ♀ $D^2 (D \times a) (DR)$	$\times$ *blw.* ♂ $a (DR)$	2 *bl.* 1 *br.* 2 *blw.*
(35)	,,	$\times$ *w.* ♂ ϵ	1 *bl.* 1 *br.* 3 *blw.* 2 *w.* (4 eaten)
(36)	,,	$\times$ *brw.* ♂ $C^{2\cdot 2} (DD) (C^2 \times a)$	3 *bl.* 2 *br.* 1 *blw.* (3 eaten)
(37)	*br.* ♀ $D^3 (D \times a) (DR)$	$\times$ *blw.* ♂ $a (DR)$	2 *bl.* 1 *br.* 3 *w.*
(38)	,,	$\times$ *brw.* ♂ $\gamma (DR)$	3 *br.* 2 *brw.* 3 *w.*
(39)	,,	$\times$ *w.* ♂ ϵ	1 *bl.* 1 *blw.* 1 *brw.* 2 *w.*
(40)	*w.* ♀ $B^{2\cdot 1} (B^2 \times a)$	$\times$ *blw.* ♂ $a (DR)$	— 2 *blw.* 3 *w.* (3 eaten)
(41)	,,	$\times$,,	— — 5 *w.*
(42)	*blw.* ♀ $C^{1\cdot 2} (C^1 \times a) (DR)$	$\times$ *blw.* ♂ $a (DR)$	— 7 *blw.* —
(43)	,,	$\times$,,	— 4 *blw.* 2 *w.*
(44)	*blw.* ♀ $C^{1\cdot 3} (C^1 \times \epsilon) (DR)$	$\times$ *brw.* ♂ $\gamma (B \times a) (DR)$	— 7 *blw.* 1 *w.*
(45)	*blw.* ♀ $D^{2\cdot 3} (D^2 \times a)$	$\times$ *blw.* ♂ $a (DR)$	— 5 *blw.* —
(46)	*blw.* ♀ $D^{3\cdot 3} (D^3 \times a)$	$\times$ *brw.* ♂ $C^{2\cdot 2} (C^2 \times a) (DD)$	1 *bl.* 1 *br.* 1 *blw.* (1 died)
(47)	*bl.* ♀ $D^{1\cdot 1} (D^1 \times a) (DR)$	$\times$ *w.* ♂ ϵ	1 *bl.* 2 *blw.* 2 *w.*
(48)	*blw.* ♀ $C^{1\cdot 2\cdot 1} (C^{1\cdot 2} \times a)$	$\times$ *blw.* ♂ $a (DR)$	— 5 *blw.* —
(49)	*blw.* ♀ $C^{1\cdot 2\cdot 2} (C^{1\cdot 2} \times a)$	$\times$ *blw.* ♂ $a (DR)$	— 7 *blw.* —
(50)	*blw.* ♀ $C^{1\cdot 2\cdot 2\cdot 1} (C^{1\cdot 2\cdot 2} \times a)$	$\times$ *blw.* ♂ $a (DR)$	— 4 *blw.* —

The mice originally introduced were 5 albino females, 2 albino males, 1 black-and-white male, and 1 black-and-white female, all of unknown extraction.

Several albinos were produced in the experiments. Mated with albinos they gave albinos only (41 in all). The original *blw.* ♂ *a* was heterozygous, containing albino, but the *blw.* ♀ *C* probably did not, though the figures are insufficient for proof. Both of the original *blw.* on mating with albino gave rise to some *brown* or brown[1]-and-white offspring, and were probably giving off gametes of this nature. All such specimens were alike in tint except one which was distinctly lighter.

The families of the albino *D* (Expts. 10–14) are especially interesting; for, as Mr Parsons pointed out to me, all the 13 coloured offspring by two different *broken*-coloured males, one *brw.*, the other *blw.*, were *self*-coloured, brown, or black. This result resembles one obtained by Castle ((5) p. 542), but the suggestion that such a pied individual is a mosaic which throws self-colour gametes is not readily applicable to this case. For here the peculiarity evidently lies in the gametes of the individual albino, since with other albinos the same males gave pied offspring. As Castle commonly obtained such self-coloured mice from albinos crossed with pied, it is likely that the

[1] Microscopical examination of a specimen kindly sent by Mr Parsons proved this colour to be "chocolate."

peculiarity may belong to certain strains of albinos. The detailed account of his experiments, which is promised, may perhaps give an indication on this point.

Parsons' cases give besides some indications as to the ratios of the gametes. It will be seen that the relation of brown to black is not merely that of dominant and recessive, for either may give either. Nor can it be supposed that the brown is a mere heterozygous form. Each colour, whether self or pied, may be dominant over albino, and the figures show pretty clearly that in the *blw.* ♂ α the albino gametes equalled the browns and the blacks collectively, for with various albinos he gave 27 coloured (*q.v.*), 31 albinos, a near approach to equality. As regards the *brw.* ♂ γ, the evidence is that with 3 albinos he gave 11 coloured, 19 albinos. On the other hand, 4 heterozygous coloured females × *w.* ♂ ϵ gave 16 coloured, 7 albinos. As the result of the reciprocity of these numbers, the total (adding Expt. 23) of coloured to albinos, produced by all matings in the form $DR \times R$, is exactly 59 to 59. It is, however, difficult to believe that the departure from equality just named is simply fortuitous, for it is in each case steadily maintained through a series of families. If the figures are grouped according to mothers (instead of fathers, as here) these peculiarities are partly lost, but further experiment may possibly indicate that different kinds of heterozygotes are here to be distinguished.

Of matings in the form $DR \times DR$ there are ten cases, Expts. 26–7, 32–4, 37–8, 42–4, giving a total of 49 coloured, 14 albinos, the simple Mendelian expectation being 47·25 to 15·75.

In these experiments there is also good evidence of the appearance of dominants containing no albino, for example *brw.* ♂ ($C^{2\cdot 2}$), and probably *blw.* C^1.

Information given me by Mr J. Wilton Steer and Mr Atlee, and the experiments lately begun by Miss Durham and Mr Staples-Browne, enable me to add a few indications as to the probable specific behaviour of some of the colour-types in crossing, though these have at present only the value of hints for further experiment.

The agouti (*Mus musculus* colour) is of course dominant to albino, but so far has not been resolved in F_2, having apparently the same behaviour as the wild colour in Cuénot's experiments, but sometimes piebalds of agouti and white appear.

Yellow and black crossed have given sables or "dingy fawns[1]."

[1] More recently Miss Durham has thus bred some full *blacks*. Reliable and extensive information as to the result of mating yellows with blacks is greatly needed.

Chocolate × albino may give, according to Mr Steer, the wild *musculus* colour, doubtless by reappearance of the black pigment in association with brown of the chocolates. Probably the strains used had other differences also (cf. p. 105). Miss Durham has found chocolate a simple dominant over albino.

Sable × black-and-white, according to the same authority, has given sables, though in this case the result will probably be found to differ according as the black-and-white is homo- or hetero-zygous.

Sables bred together have given sable, black, and dingy fawn in the same litter.

Blue × albino has given a full black, sometimes with white patches on tail.

Two yellows (from an inbred strain 4 years old) gave 1 yellow and 2 chocolates (Steer). This last occurrence is unexpected and needs careful verification.

Variegated black-and-white × chocolate-and-white gave on one occasion (Steer) 5 black-eyed whites and 1 chocolate-and-white.

As mentioned above, blue may be recessive to black and breed true from its first appearance, and will doubtless prove to be a homozygous colour.

We may now pass to a consideration of the crosses made with "Japanese" waltzing mice. The exact physiological nature of the waltzing habit seems to be still uncertain. Reference to the work especially of Cyon, Rawitz, and Zoth shows that, though malformation of the labyrinth is not infrequently associated with this condition, at least the degree of the structural malformation varies considerably.

The origin of the variation is still more obscure. Mouse-fanciers have assured me that something like it may appear in strains inbred from the normal type, though I cannot find an indubitable case. Such an occurrence may also be nothing but the appearance of a rare recessive form. Certainly it is not a *necessary* consequence of in-breeding, witness von Guaita's long series of inbred albinos. From analogy with other cases, we should be prepared to find that the existence of such a structural feature in one of the gametes had an effect on the colour of the heterozygote; but the evidence, as we shall see, is on the whole unfavourable to this view.

As to crossing of waltzers and albinos, the earliest evidence is that of Haacke, whose records are qualitative only. Crossing waltzers, blue-grey with white marks, and albinos, he obtained mice generally

self-grey (? agouti), more rarely self-black. Their offspring occasionally had a small white mark on the ventral surface.

The next large body of evidence is that of von Guaita (19), who used black-and-white waltzers with dark eyes (von Guaita *in litt.*) and an inbred strain of ordinary albinos. From this cross, F_1 was always (from 4 pairs) a self-coloured house-mouse, and was also like that wild type in size (being larger than the waltzer and smaller than the albino) and in wild disposition. F_2, raised from F_1 bred *inter se*, consisted of albinos and 4 coloured types—black, grey, black-and-white, grey-and-white. The totals were 30 coloured, 14 albinos. On the expectation of 3 : 1 there should have been 33 and 11, so that the excess of albinos is distinct, though the numbers are small; but when all *certain* cases of $DR \times DR$ (taking albino as R) are included, the numbers are 117 coloured and 43 albinos, coming very near indeed to the expectation 120 to 40. There can therefore be no doubt that the heterozygotes produced on an average equal numbers of albino gametes, and of gametes bearing the various colour-types.

There are only two matings certainly in the form $DR \times R$. These gave 23 + 1 coloured, 20 + 1 albinos, closely approaching the expected equality.

In (20) Table I, from 1st and 5th pairs, we have families of 17 coloured and 13 coloured respectively, showing pretty clearly that some of the coloured individuals contained no albino. As far as the few observations went, the extracted albinos gave only albinos. So far therefore the Mendelian hypothesis harmonises well with the phenomena.

When, however, we begin to consider the relations of the several colour-types to each other, we meet some important problems. The original waltzers are described as black-and-white. Of what pigments the black was made up we do not know. Probably it contained both the black and the brown elements. However this may have been, the reversionary heterozygote clearly did, though whether it also contained the *yellow* pigment is not so clear.

On examining the details as to the offspring of the several pairs, it appears that though the self-greys may, as the first cross proves, contain all the other 3-coloured types and the albino, the grey-and-white contain the albino only. Similarly the black-and-white can only contain the albino, so far as the evidence goes. But black seems to be dominant over black-and-white.

The facts are not sufficient to make these deductions quite certain; and, in particular, since the evidence in rats shows that grey-and-

white may dominate over black-and-white, it may be merely from accident in the choice of individuals that no black-and-white was produced by any of the grey-and-white mice.

The families from the 4th pair on Table I, and from the 3rd pair on Table II, are especially interesting as giving indications as to the gametic ratios in a complex case, though the evidence is insufficient to determine these ratios. In the first case black-and-white × black gave 10 black, 15 black-and-white, 7 albino. Both parents were heterozygotes containing albino, being each raised from self-greys × white. From the facts it is clear that one parent at least was giving off gametes black, black-and-white, and white; and from the indication that black is dominant to black-and-white, it is probable that this parent was the black. The simplest supposition is, then, that the black-and-white gave off *blw.* and *w.*, and that the black gave off *bl.* and *blw.* in equal numbers, and whites equal to their sum. This distribution would give the ratio

1 *bl.* : 2 *blw.* : 1 *w.*,

and where experiment gave

10 *bl.* : 15 *blw.* : 7 *w.*

we should expect 8 *bl.* : 16 *blw.* : 8 *w.*,

which fits well. But in the 3rd pair on Table II we have a *bl.* × albino giving

7 *bl.* : 16 *blw.* : 20 *w.*,

where, on the hypothesis suggested, we should expect *equality* between *bl.* and *blw.*, and the discrepancy is considerable and emphatic.

Pending further experiment, the relations of *bl.* to *blw.* and to white cannot be stated with any confidence. Another point calling for elucidation is the distinction between the black-and-white of the original waltzers and the black-and-white of subsequent generations. F_1 from albino and the waltzers was the atavistic grey, but there is no indication that the subsequent heterozygotes between *blw.* and albino were grey; or more strictly there is a great deal of evidence that they were usually *blw.* The suggestion also that the atavistic colour was due to the union of the waltzing and non-waltzing character seems to be plainly excluded, because even normal albinos in later generations proved to be heterozygotes of waltzing and non-waltzing gametes. At present, therefore, we cannot declare what was *the* difference between the original pure gametes which caused the reversion when they were united.

Lastly, there is a difficulty, perhaps the most serious of all, in the result of the union of albino × self-grey ((19) p. 328, 2nd pair, both parents being in F_2) which gave 13 grey, 3 grey-and-white. I see at present no suggestion as to the gametic production of the grey parent in this case which can be made with any probability, consistently witb the other facts. Possibly the diversity of gametes lay with the albino.

I now pass to an examination of the evidence of Darbishire, who crossed ordinary albino mice with waltzers. The waltzers used were "pale fawn"-and-white with *pink* eyes, thus outwardly corresponding somewhat with one of the breeds of rabbits called "Himalayan." The nature of the pigmentation described as "fawn" is not specified; but from the results, and especially from the distinction drawn by the author between "fawn," "fawn-yellow," and "yellow," there can be little doubt that the fawn was composed of both yellow pigment and a dark pigment, probably black. Twenty-nine pairs were used in the production of F_1. The offspring of 23 of these pairs, 120 individuals, had grey colour. All except one had more or less white or whitish, differing in extent. Some had more white than the waltzers, while in others the whitish colour only appeared on the belly. The pure albinos gave on the whole more fully coloured, the extracted albinos less fully coloured heterozygotes. The tint of the grey is further classified into "pale wild colour" and "dark wild colour," both being stated to he such as occur in *musculus.* Full details as to distribution are given (*q.v.*).

Of the remaining 6 pairs, 4 gave one or more mice with the colour-patches *black* (with grey brethren in three families) as follows:

Pair	*Patches* *Grey*	*Patches* *Black*
XXVII	–	1
LXXVII	6	2
LXXVIII	1	3
LXXXV	4	3
	11	9

Lastly, two pairs gave both greys and yellows, thus:

Pair	*Patches* *Grey*	*Patches* *Yellow*
XII	3	2
LXXXIV	4	5
	7	7

In the original account and in the discussion of the facts by Professor Weldon in *Nature*, the offspring of the 29 families are referred to as having consisted of a mixture of greys, yellows, and blacks; and the fact that only certain families gave blacks and certain families yellows, and that no family gave both blacks and yellows, is not emphasised. We can conceive that both yellows and blacks *might* be associated with greys when "fawns" are crossed with albinos, but till the phenomenon occurs it need not be considered in this connection[1].

To proceed with the fundamentally important question of the purity of the coloured race, we are informed that the original waltzers were bred together for some months and gave only offspring like themselves. The number of individuals thus tested and the number of offspring raised from them are not given, but we may conclude that they were considerable. When, however, we regard this evidence of purity in the light of the facts provided by the 6 families which gave either yellows or blacks, we perceive that if "fawn" is dominant to yellow and to black, the occurrence of yellows and blacks in the crosses with albino is readily explained. We have in fact only to suppose that in family 27 the coloured mother, and in families 77, 78, 85 the coloured fathers, contained *black*; and that in families 12 and 84 the coloured fathers contained *yellow*; and the results are fairly clear. The chance of seeing the impurity by merely crossing fawns together would not be very great. Most of them evidently were pure, and since black × yellow certainly *may* give a dingy fawn heterozygote, the impurity would probably not be demonstrated unless fawns containing black bred together, or fawns containing yellow bred together. By breeding the mother of family 27 with the father of 77, 78, or 85, some test of this suggestion might have been made. Of course we have as yet no direct experimental proof that fawn is dominant to black and to yellow; but since sables can throw blacks, and since in rats grey-and-white is dominant to black-and-white, it seems very possible that these "fawns" may also have been thus dominant.

[1] When a compound character is crossed with a recessive, it sometimes happens that *components of the compound appear already resolved in members of* F_1. *For* example, I have seen the "walnut" comb of the pure Malay fowl (which can be produced by synthesis of rose-comb and pea-comb in a more or less stable union) crossed with single comb give some rose, some pea, some walnut, as well as some single. Such a phenomenon will probably be demonstrated to be a *partial* monolepsis ("false hybridism"), and zygotes exhibiting the several components will probably not reproduce the excluded elements in their posterity.

The most striking fact about the F_1 heterozygotes (not mentioned in Darbishire's first paper) is that they all had *dark* eyes, though both parents had pink eyes. The albino showed itself a recessive as usual. Moreover, just as in von Guaita's case, the colour of the waltzers did not behave as a simple dominant, but formed a specific and reversionary heterozygote. It is especially interesting that this heterozygote should have been so nearly the same[1], though Darbishire's original coloured form was "fawn"-and-white, while von Guaita's was black-and-white. This certainly suggests that the *completeness* of the reversion may have been due to the meeting of some other dissimilarities than those indicated simply by colour and albinism (cf. Steer's case of chocolates, p. 92). Other facts point in the same direction.

Moreover, if the "fawn-yellow" of Darbishire's class *b* is the same colour[2] as the pale fawn of the original waltzers, it is curious to find that in F_2 there were black-eyed (therefore presumably heterozygous) "fawn-yellows," when the colour *grey* would have been the natural expectation. This phenomenon may be compared with that seen in von Guaita's work, where original black-and-white × albino gave greys; and in F_2 black-and-white may be a simple dominant over albino. (Compare also Parsons' evidence as to chocolate (= brown) with Steer's experience.)

The result of mating the wild-coloured F_1 together, as far as the detailed tabulation extended, was:

Albino	9	All pink-eyed
Yellow	4	3 pink-eyed
Fawn-yellow	6	3 pink-eyed
Pale grey	9	
Dark grey	1	
Black	5	
"Lilac"[3]	3	1 pink-eyed
	37	

In all, therefore, 16 were pink-eyed and 21 dark-eyed, when equality is expected.

[1] Darbishire's being, however, mostly pied, while von Guaita's were selfs.

[2] Until qualitative details of these colorations are published, their exact nature can only be surmised.

[3] [From a specimen exhibited by Mr Darbishire, I think this colour is probably one of the dilutions of *brown* pigment. It appeared to be a paler shade of the "silver" of fanciers.]

A postscript gives the number raised in F_2 (presumably from *wild* coloured F_1) as increased to 66, and though the individuals are not classified according to colours, the information is given that there were—

	Albinos pink-eyed	Coloured pink-eyed	Coloured (? all) dark-eyed
	13	17	36
the expectation being	16·5	16·5	33

Before attempting further to analyse these facts, the results of wild-coloured $F_1 \times$ albino must be given. In the body of the paper 88 young so produced are recorded, viz. 39 albino, 31 wild-coloured (18 darker, 13 lighter), 15 black, 3 yellow. The total increased subsequently to 205, of which 111 were albinos and 94 had some colour in their coats, the specific colours not being as yet given. All the coloured individuals from this mating were dark-eyed, as would be expected. In accordance with the other results we should expect—

	105·5 albinos	and	105·5 coloured	with dark eyes,
where experiment gave	111	,,	94	,, ,, ,,

It is therefore clear that if we regard the gametes of F_1 as consisting of two kinds, colour-bearing and albino, in equal numbers on an average, this simple form of the Mendelian hypothesis fits the facts very closely, and the distribution of albinism and eye-colour is approximately what that hypothesis leads us to anticipate. When, however, we try to assign the ratios of the several colour-gametes *to each other*, and to determine the specific results of their unions, we encounter certain difficulties, though in all probability further experiment will enable us to make this analysis complete.

So far we have no knowledge of the specific composition of the several types seen in F_2, and until they are bred separately *inter se* we can only predict the offspring with reserve. Any such prediction can only be made on the hypothesis that the regularity of the behaviour has been maintained, and that no original variation or mutation arises (as may happen for instance in peas and perhaps sweet peas). We must also expect some irregularities from the fact already mentioned, that the several families in F_1 were not all comparable, and in subsequent generations it will be necessary to distinguish members of black-giving, or of yellow-giving families from the

rest. Subject to these provisos, we expect the pink-eyed coloured types to give only pink-eyed when bred *inter se* and no albinos[1], but that the dark-eyed will give both pink-eyed and dark-eyed; and that some of the offspring of dark-eyed mated *inter se* (or with albinos) will be albinos. The pink-eyed coloured forms mated with pure albinos will presumably give all dark-eyed offspring again[2].

Similarly, taking the types of F_2 singly, it is likely that dark-eyed yellows will give only yellows, perhaps creams, and albinos, while the dark-eyed blacks should give only blacks, perhaps blues, and albinos. The dark-eyed greys will probably give both blacks and yellows, though in view of von Guaita's evidence that grey may exist as a new homozygote, this is perhaps doubtful. As far as the published evidence goes, the most probable constitution of the several forms in F_2 is as follows:

Albinos	albino × albino
Pink-eyed yellows	yellow × yellow
Dark-eyed	yellow × albinos
Pink-eyed fawn-yellows	fawn-yellow × fawn-yellow
Dark-eyed blacks	black × albino (?)
Dark-eyed greys	fawn × albinos (and perhaps some other combinations)
Pink-eyed lilacs	lilac × lilac.

The absence of blacks with pink eyes is noticeable, and raises the question whether there is not a permanent synthesis in these blacks.

Finally, we have two important problems, the nature of the *dark*-eyed fawn-yellows and of the *dark*-eyed "lilacs." As they are dark-eyed they presumably both contain albino. But as regards the first, it is difficult to see what the other gamete can be in that case. For from F_1 we learn that fawn × albino gives *grey*, not fawn-yellow. On the other hand, as there are black and yellow gametes, we ought to find their heterozygote, which will presumably be *fawn*. But if this combination follows the rules of the others, the heterozygote should

[1] Unless the phenomenon seen in the albino guinea-pig occurs.

[2] In Mr Darbishire's third report (28) just published it is recorded that a pink-eyed yellow-and-white in F_2 bred with albinos gave 8 *albinos*, 11 grey-and-white, 1 yellow-and-white. The occurrence of albinos from this mating is of course a proof that the constitution of the pink-eyed yellow was in this case not that suggested in the present text. Experiments with other coloured members of F_2 are not yet given. The relation of the yellows to the rest must be regarded for the present as quite unknown. It may be remarked that yellow-and-white varieties both of rabbits, fowls, and pigeons are often peculiar in their inheritance, and rarely breed true for many generations.—July, 1903.

be pink-eyed, not dark-eyed. The number of dark-eyed fawn-yellows, three, is too few to make it likely that these are the black × yellows, which we expect to appear as a fairly frequent combination; and the general indications are quite unfavourable to the view that any considerable number of heterozygotes can be dark-eyed without the presence of the albino, though it is not impossible that such real synthesis may take place.

Next the "lilacs" raise certain questions[1]. We must suppose that the dark-eyed "lilacs" contain albino; but in the offspring of F_1 × albino there are no "lilacs." As F_1 is giving off gametes capable of forming "lilacs," we see that the lilac × pure albino gives some other colour. Next, which of the groups can be supposed to represent the lilac-bearing gametes in their other combinations? This also is a question we cannot answer.

A similar difficulty is created by the scarcity of yellows in the offspring of F_1 × albino. There were only 3 in 88. We might have expected the numbers of yellows and blacks to be equal, but there were 15 blacks. Moreover, all the yellows were in *one* family. So far this is quite inexplicable. It probably indicates that some of the albinos possessed powers of resolution different from those of others, or conversely that some of the original "fawns" were more easily resoluble than others. [Cf. Cuénot's new results (27), where blacks were resolved out, but apparently *no* yellows.]

A line of inquiry is suggested by the miscellaneous constitution of F_1. We have seen that all members of F_1 are not alike, and it is not impossible that the greys from families which give no blacks or yellows may be different in constitution from greys in families which gave one or the other. If the individuality of the several parents of F_2 were given, this possibility could be examined. The fact that an original waltzer was giving off yellow or black gametes might be an indication that resolution of characters had already begun; and perhaps therefore the F_1 from different families, though alike grey, may be in some measure heterogeneous. In these cases it is most important that each individual parent and its offspring should be separately traceable.

It is not impossible that some light on these questions could be obtained by noting the sexes in which the several forms appear.

[1] [Subsequently Darbishire (*Biometrika*, III, 1904, p. 14) stated that he had never seen dark-eyed lilacs, and that his earlier record of them was probably due to an error. ED.]

In view of the facts I do not understand the meaning of Darbishire's statement that "the inheritance of eye-colour is not in accordance with Mendel's results[1]." So far as the experiments are yet recorded, the behaviour of the eye-colour is typically Mendelian, and follows Mendelian expectation in its simplest form. The occurrence of albinos is similarly Mendelian, one albino in four being plainly indicated as the average from $F_1 \times F_1$[2].

As we have also seen, the colours taken collectively follow simple expectation; $F_1 \times F_1$ giving approximately 3 coloured to 1 albino, and $F_1 \times$ albino giving approximately equal numbers of each.

[1] For further criticism of this statement see Castle and Allen (7).

[2] As regards the waltzing character von Guaita's experiments agree with Darbishire's in showing that it was always recessive to the normal. No individual in F_1, or in families produced by crossing F_1 with the pure normal, waltzed. In Darbishire's experiments $F_1 \times F_1$ gave 8 waltzers in 37 offspring, indicating 1 in 4 as the probable average. $DR \times R$ is not recorded. From von Guaita's matings in the form $DR \times DR$ the totals of families were 117 normal and 21 waltzers made up as follows:

Normal	*Waltzers*
36	8
14	2
25	7
41	2
1	2
117	21

There is therefore a large excess of normals over the expected 3 to 1. This is possibly due to the delicacy of the waltzers, which are certainly much more difficult to rear than normals are. The small numbers in von Guaita's litters make it very likely that many were lost before such a character as this could be determined. On the other hand, we have to bear in mind that as the presence of waltzers is here the only proof that the matings were in the form $DR \times DR$, it is possible that the total of normals should really include some families which gave normals only.

$DR \times R$ gave 18 normal and 10 waltzers distributed in families thus:

Normal	*Waltzers*
3	4
3	2
10	3
2	1
18	10

Here the same paucity of recessives is noticeable.

Von Guaita did not succeed in raising any offspring from extracted waltzers bred *inter se*.

All that can be positively asserted is that the qualitative result is in full agreement with the Mendelian expectation based on the absence of waltzers in F_1, and that it is not impossible that there may be the expected equality in number between D and R gametes produced by F_1.

As to the frequencies and valencies of the particular colours nothing can be said with much confidence as yet, beyond the statement that F_1 gives off albino gametes about equal in number to the various coloured gametes collectively. In a discussion of this subject, Professor Weldon (25) has suggested that an average of *one albino in nine* might have been expected. I can see no reason why this proportion should be impossible in nature, from $F_1 \times F_1$. Its occurrence would, however, be remarkable and raise some important problems in gametogenesis. So far, however, it has not been recorded. Professor Weldon is in error in stating ((25) p. 34) that I have already dealt ((4) p. 52) with such a case of 1 albino in 9. The case in question was that of *Antirrhinum*, where de Vries obtained from $F_1 \times F_1$ four forms in the proportion 9 : 3 : 3 : 1, the *one* being the white, which therefore occurred in the proportion of 1 in 16. This is the proportion Mendel himself conjectured might be found in a case of resolution, but I do not gather that he had actually observed such a case.

No case of resolution has yet been sufficiently studied for us to speak with any confidence as to the ratios of the gametes or the nature of the process of resolution. Tschermak has had cases of 1 recessive in 4, after resolution. In poultry I have had cases somewhat similar, to be described hereafter.

In apparently all recorded cases of resolution some gametes of F_1 carry the compound character unresolved. It is not at all easy to suggest a scheme which shall fit both the observed facts of resolution and those of cell-division. For example, suppose the gametes of F_1 to be 50 per cent. albino, 50 per cent. variously coloured, if segregation were complete. Let us consider the coloured gametes separately, and for simplicity assume there are only three kinds of them, viz. the unresolved grey, black, and yellow, the two latter being hypallelomorphs of grey. It is then clear that in whatever numbers the three types are each represented, so long as their sum equals the total of albino gametes, there must be more black character in any black gamete, and more yellow in the yellow gamete, than in any grey gamete; *or* there must somewhere be a cell-division in which a part of the yellow and a part of the black have been lost. If, for instance, the hybrid bore gametes in the proportions

2 grey (= black + yellow), 1 black, 1 yellow, 4 albino,

we recognise that unless the blacks and yellows carry double portions of their respective colours, part of the colour originally introduced

into F_1 has been lost. Such doubling is not altogether inconceivable, though until histological methods are made applicable to these questions of gametogenesis the possibility can hardly be tested. We note as a fact favourable to such a view, that the visible amount of pigment in a black or a yellow zygote is far greater than the amount of the same pigment in the original compound colour. But this consideration cannot be allowed much weight, seeing that there may be an excess of pigment in *heterozygotes* produced even from two gametes apparently bearing no pigment elements at all (cf. p. 81). In the chemistry of pigmentation there may perhaps be interactions and cancellings so complex as to make this particular problem as yet quite insoluble.

Fuller analysis is especially needed also to determine the place of the pied and diluted colour-bearing gametes in the series, but it is fairly certain that they must be regarded as due to disintegration and imperfection of resolution of the colour from the albino character.

Future experiment must decide the conditions determining resolution. Cuénot, as I understand his paper, got none in the main experiment with wild mice; but he states that he obtained yellows, blacks, and pieds "*accessoirement*" (perhaps by introducing some coloured fancy strain?).

From this survey of evidence mostly already published, it is clear that Mendelian analysis provides a means of elucidating a large part of the phenomena. The majority of the observations are in accord with the Mendelian hypothesis in a simple form. The true solution of several subordinate problems still remains obscure. The value of the Mendelian analysis will be the more appreciated when it is remembered that previously the whole body of facts must have been regarded as a hopeless entanglement of contradictions, as reference to any non-Mendelian discussion even of these very phenomena will show.

As I have elsewhere pointed out, the central phenomenon in Mendelian heredity is segregation. The characters in simplest cases are treated as units in gametogenesis. In more complex cases there is resolution, sometimes also disintegration and imperfect segregation, leading to the formation of fresh units. The gametes bearing these units are produced in numerical proportions which on an average are also definite, but as yet these proportions have only been determined in the simple cases. There is no doubt that further experiment will determine them in complex cases also.

It is the object of Mendelian analysis to determine

(1) the constitution of the several types of gamete produced by each type of zygote;

(2) the numerical proportions in which each type of gamete is produced;

(3) the specific result of the union of any two of the types of gamete in fertilisation.

Though for convenience we may still speak of inheritance as being "Mendelian" or "non-Mendelian," we are rapidly passing out of the initial phase of the inquiry in which such expressions are demanded. In our further investigations we are concerned not so much with the question of the applicability of the simplest Mendelian hypothesis to special cases, as with the formulation of the specific laws followed by the several characters of various animals and plants in gametogenesis and in union by fertilisation. As in chemistry, these laws must be worked out separately case by case, and each as it is determined has the value rather of fact than of hypothesis.

In dealing with this class of fact, special precautions are necessary in order to establish the identity and purity of any variety chosen for experiment. From the description of the varieties of mice given at p. 78 it will be seen that some colours may be easily confounded in description, though the pigments on which they depend have a different chemical behaviour. This is especially the case with regard to "fawn," "fawn-yellow," and "yellow." In such cases it is absolutely necessary that the presence or absence of *dark* pigment should be noted, and that some attempt should be made to distinguish the two dark pigments from each other.

In all attempts to trace laws of colour-heredity, colours of the various parts will usually have to be reckoned with. In horses, for example, the general hody-colour, without that of the mane, tail, and fetlocks, is likely to be an insufficient guide to the heredity. In man the heredity of eye-colour cannot be sufficiently investigated if it be separated from the colour of the hair, and so forth. For the present, therefore, Professor Pearson's conclusion that the Mendelian system does not apply to coat-colour of horses or to eye-colour in man should not be received without reserve. By neglect of the precautions named above many results may be described as conflicting with each other, which further analysis would show to be harmonious.

[*Note added July*, 1903

When this communication was read I had not seen the important paper of Cuénot (27) dated March 1903. He states that grey mice of his F_3 when crossed with albino gave several *blacks*. These, when bred with certain albinos, produced black heterozygotes, which bred *inter se* gave the Mendelian 3 black to 1 albino. Some of these latter blacks were then homozygous, and from them a pure strain of blacks was raised. This strain crossed witb wild *musculus* behaved as a simple recessive, giving grey F_1, with Mendelian ratios 3 grey to 1 black, or 1 grey to 1 black in F_2, according as F_1 was mated with F_1 or with black.

Tbe fact that the original black did not appear in F_2 or in F_3 calls for elucidation. It suggests a possible difference between the albinos used either in producing F_1 or later, some individuals having the power of resolving the grey, while others had not that power.

Cuénot next records the new and important fact that the colour of the F_1 produced from his black strain × albino differed according to the class of albino used. (1) Albinos extracted from the cross with wild grey gave *grey* F_1. (2) Albinos extracted from the cross with black gave *black* F_1. (3) Albinos extracted from a cross with yellows (of complex origin) gave a mixture in F_1, either of *yellows and greys*, or of *yellows and blacks*. There is therefore a proof that individual albinos, though outwardly alike, may belong to several distinct classes, exhibiting different properties in their heterozygous unions (cf. Parsons' case, p. 90). The resemblance of the heterozygote to the coloured type from which the albino was extracted is a new fact, the significance of which we cannot yet fully appreciate[1]. Cuénot tentatively makes the attractive suggestion that the particular colour of the heterozygote may depend on the association in the same zygote of various colour-constituents; and that though the albino is white in itself, it may carry on such constituents from a previous coloured parent. Then, according as one or other of these complementary constituents is brought in by the albino, the heterozygote will show the corresponding colour. The chief obstacle to this view is the fact that when a heterozygote shows reversion (as opposed to simple dominance) the reversion frequently includes *various* qualities, such as size, temperament, habit of growth, etc., as well as colour.

[1] Possibly it is to this phenomenon that Crampe refers in the statement discussed on p. 84 of this paper. I cannot, however, find a case of Crampe's exhibiting Cuénot's phenomenon.

A cognate problem was alluded to (p. 94) in the discussion of von Guaita's facts. His original black-and-white × albino gave a reversionary heterozygote; yet in F_2 both the black-and-white and the grey-and-white *DR*'s present those colours as simple dominants over albino, as their offspring proved. Since in this case no new strain was introduced, the reference to pedigree is not sufficient to elucidate the whole difficulty.

The relation of the several classes of albinos to each other seems to be the next point for investigation, and a useful experiment might be made by breeding albinos extracted from one colour, with albinos extracted from another colour, the offspring to be then tested with a single pure coloured race. It is not impossible that the various types of albino will then themselves exhibit phenomena of segregation.

The new report of Mr Darbishire (28) and Professor Weldon's comment (29) have appeared too late for adequate discussion here. It may, however, be remarked that both autbors scarcely appreciate the Mendelian view when they state that according to it all albinos (or other recessives) may be treated as "in every respect similar." No one, I imagine, would suppose that the similarity need extend to characters other than the albinism. We are familiar with cases in which recessives, though alike in the recessive character, are dissimilar in other respects; and (as stated *supra*, p. 81) may, when crossed together, even produce heterozygotes exhibiting a character known to be dominant over the particular recessive concerned. We should no more suppose all albino mice to be identical because they were albino, than all white sweet peas because they were white, or all glabrous stocks because they were glabrous.

Professor Weldon's appeal for the precise gametic formula of F_1 must at present go unanswered. Pending analysis of the various coloured types in F_2, no one could give the statistical composition of the gametes of F_1 so far as coat-colour is concerned; and though the general composition of F_2 agrees closely with simple Mendelian expectation, the particular composition of the various types is a question that further experiment must decide. To take only one possibility, imperfect segregation is often seen in such cases of complex resolution. No criterion save the actual production of F_3 from F_2 can show whether any of the types of F_2 illustrate this phenomenon. When such evidence is forthcoming there is every likelihood that both the qualitative and quantitative composition of the gametes of F_1 will be determinable with approximate accuracy.]

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MENDEL'S PRINCIPLES OF HEREDITY IN MICE

[*Nature*, LXVII, 1903]

THE experiments respecting heredity in mice conducted by Mr Darbishire in the Oxford Laboratory at Professor Weldon's suggestion, and described in *Biometrika*, II, pts 1 and 2, are of exceptional interest. As the fruitful development of these and similar experiments depends on a true interpretation of the facts so far reached, I offer a few words in supplement to the conclusions deduced by the author.

By crossing Japanese waltzing mice having pale fawn and white coats and pink eyes with ordinary white pink-eyed mice, 154 offspring were produced, of which 137 were grey and white, 1 was grey, 7 were yellow and whitish, 9 black and white or whitish. The colour-patches showed decided variations in amount and in tint. A fact of extraordinary physiological significance (omitted from the preliminary account) is that though the eyes of both parent-forms were pink, the cross-breds *without exception had dark eyes*, a result which, though to some extent paralleled by certain plant cases, is probably as yet unique among animals, at least in degree.

The cross-breds bred *inter se* gave 66 mice, of which 13 were pink-eyed albinos, 17 were pink-eyed with more or less colour in the coat, and 36 were dark-eyed, some (presumably all) having colour in their coats. Bred with albinos the cross-breds gave 111 pink-eyed albinos, and 94 with dark eyes and some colour in their coats. The coat-colour phenomena, though exceedingly important, are too complex for consideration in a few lines. The evidence also, as yet, is in some respects insufficient, but did space permit, I should be glad to discuss these facts as far as they go. As to eye-colour, the phenomena are simpler, and from them the following conclusion is drawn by the author:

"The inheritance of eye-colour is not in accordance with Mendel's results. For since pink eyes occur in parti-coloured mice, the possession of pink eyes must, on Mendel's view, depend on a separate embryonic element from that which determines coat-colour. Pink eyes are, however, not 'dominant,' since the two pink-eyed parents of the first generation always produce dark-eyed young. For the same reason pink eyes are not 'recessive.' Yet although pink eyes disappear in the first generation (the result of crossing two pink-eyed parents) they reappear in the second; but a correlation is then established between coat-colour and eye-colour which is strong in the

offspring of hybrids paired together, and at present perfect in the offspring of hybrids and albinos. The behaviour of eye-colour is thus in every respect discordant with Mendel's results."

The purpose of the allusion to "dominance" escapes me. In what circumstances could pink-eye be dominant, or recessive, to pink-eye? The reference to correlation is no less perplexing. The meaning might be clearer if we were told what offspring the writer would have expected if the inheritance *had* been "in accordance with Mendel's results." But a negative conclusion, however acceptable, supplies imperfectly the place of a positive result. Let us see if a positive interpretation is compatible with the facts.

In face of so emphatic a declaration to the contrary, my opinion may seem over bold; yet I feel no hesitation in believing that the inheritance of eye-colour in these mice, so far as the record reaches, was strictly Mendelian. The first cross proves that when *in this case* an albino (pink-eye) gamete, G, meets a colour-bearing (pink-eye) gamete, G', in fertilisation we must expect the resulting heterozygote, GG', to be coloured in coat, with a *dark* eye. When these heterozygotes breed *inter se*, they will form on an average equal numbers of homozygotes, GG and $G'G'$, and of heterozygotes GG' and $G'G$. Of these, the homozygotes will all have pink eyes, but while GG will have a white coat, $G'G'$ will have some colour in the coat. The heterozygotes, GG' and $G'G$, will have dark eyes and some colour in their coats.

Treating GG' and $G'G$ as identical, we thus expect the ratio

$$1\ GG : 1\ G'G' : 2\ GG'.$$

Therefore the most probable distribution of the 66 mice is as follows:

16·5 pink-eyed albinos; 16·5 pink-eyed with colour in coat; 33 dark-eyed with colour in coat;

and the experiments gave

13 pink-eyed albinos; 17 pink-eyed with colour in coat; 36 dark-eyed (? all) with colour in coat.

Similarly, on crossing the hybrids with albinos, we expect equal numbers of GG and GG'. Therefore the most probable distribution of the 205 mice so produced is

102·5 pink-eyed albinos; 102·5 dark-eyed with colour in coat,

and the experiment gave

111 pink-eyed albinos; 94 dark-eyed with colour in coat.

Experiment agrees well with expectation. In what respect are they discordant?

The case is closely comparable with that found by Miss Saunders in *Matthiola* (*Rep. to Evol. Cttee. of Roy. Soc.*, 1902), when a white hoary form crossed with a white glabrous form gave purple hoary offspring; and with the production by Kölreuter (confirmed by Gärtner, Naudin and Godron) of purple flowered hybrids by the union of two white flowered *Daturas*, *D. ferox* and *D. lævis*. *Why* in these cases the heterozygotes are atavistic we do not know, but the problem need not be insoluble.

Anyone conversant with Mendelian phenomena can now predict the eye-colour of the future offspring of the various unions with approximate accuracy. Pending further experiments, we cannot predict the particular colours which will appear in the coats, and for various reasons we should perhaps be cautious in declaring that *all* the dark-eyed mice must show colour in their coats.

From incidental comparisons of these new facts with the simpler results of von Guaita an inexperienced reader might suppose that the two sets of experiments had been comparable and had given discrepant results. It would have prevented misconception if the author had stated that while the waltzing mice he used were pale fawn and white witb pink eyes, von Guaita's were *black and white with dark eyes*. It is a feature of the Mendelian view of heredity that different specific results may be expected when different specific materials are introduced.

MENDEL'S PRINCIPLES OF HEREDITY IN MICE

[*Nature*, LXVII, 1903]

I APPRECIATE Professor Weldon's reluctance to defend his position in a short letter[1], and I look forward with peculiar interest to the number of *Biometrika* where I gather this task will be undertaken.

Though deferring a reply on the simple matter of the eye-colour in the Oxford mice, Professor Weldon finds space to ask an "explanation" of two overlying complexities. To debate these finer points with one who doubts the Mendelian nature of the phenomena taken as a whole is like discussing the perturbations of Uranus with a philosopher who denies that the planets have orbits. Still, at the risk of diverting attention from the main issue, I will suggest how these complications may be regarded—scarcely "explained."

(1) The "lilac" mice illustrate that resolution, and partial disintegration, of characters commonly witnessed when a compound colour is crossed with an albino. The statistical value of the "lilacs" and their place in the colour-system can only be determined by further breeding. The *appearance* of "lilacs" or analogous types is what we expect, though their *absence* in the offspring of hybrids × albinos constitutes a certain problem. This and other genuine difficulties call for careful statement and analysis.

(2) The diversity of coats in the first crosses points to heterogeneity among the gametes of one or both "pure" races. The nature of that heterogeneity is the question. Each race may breed true to colour, but the cross-bred offspring of the two is not necessarily uniform. The pigment excreted by heterozygotes may, as I could easily demonstrate, depend on factors (probably determinable) other than the visible colours of the parents, and having an independent distribution amongst their gametes. Also, while we are comprehensively assured that the coloured race was pure, the precise, if as yet uncontrolled, testimony of the records that certain individuals were *not*, seems to have been overlooked. More elaborate hypotheses may be needed, but not until the simpler have been disproved.

P.S.—A reviewer declares (*Nature*, April 9) that the data in this case are "by no means easy of interpretation," on what hypothesis I know not; and that "much of the evidence is *primâ facie* in favour of ancestral inheritance." It is scarcely too much to state that in

[1] [See *Nature*, LXVII, 1903, p. 515.]

each set of matings the distribution (1) of pink and dark-eyed, (2) of coloured and albino coats, (3) of "waltzers" and non-waltzers, is in punctilious agreement with Mendelian prediction. The variety of colour in the first cross I have dealt with. Knowing something of the recent history of fancy mice, two kinds of grey in this generation cause me no surprise. In the whole evidence I can find only three real difficulties, all surely of minor importance. One is named in my letter. The second is the occurrence of three dark-eyed *fawn-yellows* in the offspring of first crosses. The third is the scarcity of yellows in the offspring of hybrids × albinos. If the individuality of the parents were declared, two, perhaps all, of these points could be cleared up. I am not acquainted with any other conception of heredity which elucidates any part of the facts.

MENDEL'S PRINCIPLES OF HEREDITY IN MICE

[*Nature*, LXVIII, 1903]

THE issues raised in the case of these mice are as yet of such a simple and familiar kind that the source of Professor Weldon's difficulty is not easy to surmise[1]. When a gamete G bearing albino and pink-eye meets a gamete G' bearing coloured coat (in this case fawn) and pink-eye, a heterozygote GG' is produced, with dark eyes and coloured coat. Such hybrids, as the experiments proved, gave off equal numbers of gametes G, bearing albino witb pink-eye, and G' bearing colour with pink-eye. Consequently from $GG' \times GG'$ we expect and obtain $GG + 2\,GG' + G'G'$; and from $GG' \times G$ equal numbers (approximately) of GG and GG'. So far, GG are pink-eyed albinos; GG' are dark-eyed with *some* colour in coat; $G'G'$ are pink-eyed, but with *some* colour in coat.

If we do not consider what *particular* colour GG' and $G'G'$ will have, we may treat all gametes G' as identical. But after crossing witb albino such a condition would be unusual. The colour brought in by the original G' is generally in part resolved, and various sorts of G' gametes are formed, viz. aG', bG', cG', $abcG'$, etc. Therefore when the hybrids breed together there will be GG' zygotes of several colours, viz. $G.aG'$, $G.bG'$, $G.cG'$, etc.; also $G'G'$ zygotes of several colours, viz. $aG'.aG'$, $aG'.bG'$, etc. Each combination will have its appropriate colour and frequency, though (if the regularity be maintained) all GG' will have dark eyes and *some* colour, and all $G'G'$ pink eyes and *some* colour. But as the hybrid produces G gametes equal in number to the various G' gametes collectively, $GG' \times GG'$ will give on an average 1 albino in 4 offspring (experiment gave 9 in 37); and there is no question of 1 in 9. We are only concerned with *one* hypothesis (that I have set forth in *Mendel's Principles of Heredity*, p. 29), and with this hypothesis the published facts are in admirable agreement.

Heterogeneous offspring from crossing two seemingly pure races may seem to Professor Weldon an "amazing" phenomenon, but it is one with which the breeder early becomes familiar. Even albinos need not be pure or their gametes heterogeneous in characters other than albinism.

[1] [*See Nature*, LXVII, *1903, p. 610.*]

ON THE INHERITANCE OF HETEROSTYLISM IN *PRIMULA*

[*Proceedings of the Royal Society*, B, LXXVI, 1905]

IN view of the results obtained by Darwin[1], Hildebrand and others, it seemed likely that the characters long-style and short-style, well known in *Primulaceæ* and other orders, might have a Mendelian inheritance. Our experiments have shown that this is the case in *P. sinensis*, the short style being dominant, the long recessive.

The inheritance is usually of the simplest type. In one case (p. 119) there was considerable divergence from the expected proportions, and it is no doubt possible that this case was one of real abnormality; but we incline to think that the irregularity was due to accident or error. But besides the cases which can be regarded as normal one individual short-styled plant gave an entirely aberrant result (p. 119); and as the offspring of this plant gave results similarly aberrant, there can be little question that we are here concerned with an inheritance of a special type. Further experiments with this family are in progress.

Another feature of interest was seen in the F_2 families raised from matings in which an *equal*-styled race was used, the phenomena well illustrating the mode of appearance of a new type by the recombination of the factors brought in by the pure parental types.

Horticultural experience as to the production of long- and short-styled offspring is in general harmony with our results. Fashion has decreed that *P. sinensis* shall be exhibited in the long-styled form alone. This being the recessive, breeds true, and short-styled plants are consequently absent from selected strains, being even difficult to procure at the present time. The florists' Auricula, on the contrary, must be exhibited in the short-styled or "thrum" form, but as this is the dominant, long-styled Auriculas continue abundant.

In the wild Primrose (*P. acaulis*, Jacq.) the two forms are about equally numerous in nature. Experiments with this species, now in progress, give indications that the inheritance of the two types follows the same rules. From the greater sterility of its illegitimate unions the Primrose is less easy to work with, and as might be expected

[1] *Forms of Flowers*, ed. 1884, giving references to the principal memoirs on the subject.

from the same cause, all short-styled wild plants so far tested, have been found to be heterozygous in respect of style.

The experiments now to be described all relate to *P. sinensis*. The inheritance of flower-colour and other characters will be dealt with in a future communication. We take this opportunity of acknowledging our indebtedness to Messrs Sutton and Sons, who have for some years placed their great collection of Primulas at our disposal, and have assisted us in many ways during the course of our inquiries.

I. Normal Cases

Long-styled × *Long-styled*

Ten such crosses were made, from which 90 offspring were raised, all long-styled. In F_2 56 offspring, all long, were raised. Various extracted long-styled recessives, fertilised by self, and by pure longs, gave 85 plants, all long[1].

Short-styled × *Short-styled*

All the four short-styled plants originally obtained for use in these experiments proved to be heterozygous. From short-styled × short-styled, 26 short and 10 long were raised, the expectation being 3 : 1. Of the 26 short some were *DD* and others *DR*. One, on self-fertilisation, gave 7 shorts. Two others, on self-fertilisation, gave 24 short, 4 long. Nine shorts raised in F_1 from long × short gave, on self-fertilisation, 120 shorts and 49 longs. The union *DR* × *DR* gave, therefore, a total of 144 short, 53 long; or, including the 36 raised between the original plants, 170 short, 63 long.

Darwin's[2] results from this form of union are valuable as indicating that he probably obtained a pure dominant. The parent short-styled plant, self-fertilised, gave 8 plants, 7 short, 1 long. The shorts, self-fertilised, gave only 2 plants which flowered (short), but the cross between short-styled and long-styled gave 15, all short.

Long ♀ × *Short* ♂, *and Reciprocal Cross*

In the first instance these crosses were all *R* × *DR* or *DR* × *R*, which gave respectively 30 short, 24 long; and 14 short, 13 long. In F_2, crosses between *DD* and *R* gave 92 all short; and *DR* × *R* gave 40 short, 48 long.

[1] Cf. Darwin, *loc. cit.* pp. 213, 214.   [2] *Loc. cit.* p. 215.

Crosses with an Equal-styled Race

Of late years a peculiar type of *P. sinensis* has been much grown, which is characterised by an extensive spreading of the central yellow eye. Instead of forming a fairly sharp pentagon as in normal flowers, the eye in this type is produced as a yellow flush extending over about half of each petal. All the strains having this flush are in the condition called by Darwin "equal-styled." The anthers are at the same level as in the long-styled flowers, and the pollen grains are small and indistinguishable from those of the long-styled. The styles, however, are short and do not reach above the level of the anthers[1]. We at first supposed that the equal-styled plants corresponded to the mid-styled type seen in trimorphic species, but this is evidently a mistake, and the relations of the three types of trimorphic forms present much greater complexity than is met with in Primula.

Experiment shows that the yellow flush is an ordinary recessive character, the ordinary or non-flushed type being dominant. The flush is transmitted independently of the length of style or the size of the pollen grains, for it may be transferred to the true short-styled or "thrum" type. But when the flush is developed in plants which by gametic composition would be long-styled, the style does not pass through the anthers, and the equal-styled condition is produced. Why the development of the yellow flush in these flowers should entail the reduction of the style, we cannot in any way suggest.

From these considerations it follows that when the equal-styled race is crossed with the true short-styled type, two allelomorphic pairs are concerned, viz. short-style (D) and long-style (R); no yellow flush (D) and yellow flush (R). F_1 is, therefore, short-styled with no yellow flush. F_2 has four types, viz. short, non-flushed; short, flushed; long, non-flushed; long, flushed, which latter is the equal-styled, the ratio being 9 : 3 : 3 : 1. The long non-flushed, which appears as a new form in F_2, is, of course, made by the recombination of the parental characters, and the meeting of the "long" character from the equal-styled parent with the non-flushed eye derived from the short-styled parent.

Equal-styled × *Equal-styled*

Four plants were raised by crossing equal-styled plants of the same

[1] Occasional flowers, in which the stigma is at the anther level, may be seen on normal long-styled plants. They are usually first flowers, and are especially frequent in *P. acaulis* in early spring. We have never seen a genuine case of mixture of types on one plant.

race, and did not differ from their parents. From these were raised 14 more by self-fertilisation, again identical with their parents.

Equal-styled × *Long-styled*

The yellow flush being recessive, F_1 is here the normal non-flushed long style; 45 such plants were first raised, all long and without the flush. In the next year, 77 such plants were produced by similar matings.

Such F_1 plants gave by self-fertilisation 183 long, non-flushed, 51 equal-styled, with the flush, the expectation being 3 : 1. Crossed with the pure recessive, they gave 93 long, non-flushed, 107 equal-styled, with the flush, numerical equality being expected.

Equal-styled × *Short-styled*

From such crosses, in which the short-styled parents were *DR*, 39 plants were raised, 19 long, 20 short, all without yellow flush. The pure short-styled plants raised in 1903, crossed with pure equal-styled plants, gave 41, all short-styled, without flush.

Such F_1 plants on self-fertilisation gave 247 plants, viz. 147 short, non-flushed, 35 short, flushed, 44 long, without flush, 21 equal flushed, the expectation being 138·9, 46·3, 46·3, 15·4.

Crossed with ordinary longs, the same F_1 plants gave 73 short, 76 long, all without flush, the expectation being equality.

The same F_1 plants, crossed with the pure equal-styled, gave 59 short, non-flushed, 39 short, flushed, 32 long, non-flushed, 24 long, flushed. This result, showing in each class a great excess of shorts, instead of numerical equality, is quite unexplained. The numbers can scarcely be taken as chance departures from equality. The same plants, however, gave recognisably normal results in both their other sets of matings, and the segregation was evidently quite normal. On the whole, it seems more likely that the aberration was due to accident, than that any novel phenomenon actually occurred in this case.

II. Abnormal Cases

With the exception just mentioned, all the cases hitherto dealt with gave fairly simple Mendelian results, but the entire series of crosses in which a certain short-styled plant (referred to as No. 6) was used showed a definite and consistent departure from normal expectation. No. 6 was a red thrum plant, obtained from a nurseryman, and we know nothing of its origin. By self-fertilisation it gave 4 shorts.

Fertilised by a short-styled plant, which had been proved to be *DR*, it gave 6 shorts, 3 longs. No. 6 was used as male on both long- and equal-styled plants, giving 10, all short-styled; but when fertilised with pollen of long- and equal-styled plants, No. 6 gave 14 short, 5 long.

The evidence so far is, therefore, that the *egg-cells* of No. 6 gave a mixture of longs and shorts, and consequently were carrying both characters, while all the plants raised from it as *male* were shorts. The numbers alone are of course too few to justify any conclusion, had it not been that a closely similar result appeared in the next generation.

By self-fertilisation No. 6 gave a short-styled plant, No. 37. This, on self-fertilisation, gave 22 shorts and no longs. Fertilised by pollen of long-styled plants, it gave 14 short, 24 long. But when used as a male parent, its pollen applied to long- and equal-styled plants gave 148 shorts and only 4 longs, of which 1 was recorded as "doubtful[1]."

Taking their offspring together, Nos. 6 and 37, when fertilised by long- and equal-styled, gave 29 long, 28 short; while when the same two plants were used as *males*, the total offspring were 184 shorts and 4 (? 3) longs. We have, therefore, the remarkable phenomenon of plants which, judged by the female gametes, were ordinary heterozygotes, while their male gametes were almost exclusively bearing the dominant character. Pending further investigation, we can offer no further comment on this singular case. It will be noted that, since the mixture was given by the *female* side, no hypothesis of parthenogenesis will meet the case.

Results of Double Pollination

In addition to the experiments described above, an attempt was made to investigate another possibility respecting the consequences of legitimate and illegitimate unions. Darwin, and after him many others, proved that in Primula more seeds are produced when plants with styles of dissimilar types are united (legitimately) than when similars are united (illegitimately). Nevertheless, illegitimate unions are not necessarily sterile, but, especially in the case of *P. sinensis*, may produce a good deal of seed.

[1] The nature of the doubt is not recorded. Until the results were added and classified no special interest had been attached to this family. Each plant as it began to flower was recorded and thrown away to make room. Probably this individual was recorded before the flower completely matured.

For examples we may refer to the average numbers given by Darwin[1]. Taking the average for legitimate unions at 100, the 13 illegitimate unions in the genus *Primula* give an average of 53 seeds per capsule, and we have found a similar proportion maintained with some constancy in our own fertilisations.

Some egg cells (about half) are therefore fertilised by illegitimate pollen, while the rest are not. This fact suggested that there may be a differentiation between egg cells of the same plant, such that some are capable of illegitimate fertilisation, others incapable.

To test this possibility, we made a large number of trials with *P. acaulis* and *sinensis*, pollinating some flowers legitimately, some illegitimately, and others with pollen of both types. We anticipated that the double pollinations, in which pollen of both types was put on the same stigma, would produce a maximum number of seeds. In the case of *P. sinensis*, by making use of the fact that green stem and pinnate leaf are recessive to red stem and palmate leaf, it was possible to arrange these double pollinations in such a way that the paternity of each resulting seedling would be apparent, and thus the number of individuals derived from each set of pollen grains could be ascertained.

This series of experiments has, however, led to no definite conclusion. They were carried out through two seasons, and an enormous number of fertilisations were made, but the resulting figures were so discrepant that we are unable to give either a positive or a negative answer to the question proposed. These discrepancies are partly due to great individual differences between plants and between flowers of the same plant, but in all probability serious irregularities were also introduced in the actual operations owing to the difficulty of applying the two sorts of pollen equally to the same stigma under really uniform conditions. If these technical difficulties could be overcome, a valuable result might possibly follow from the experiment.

[1] *Loc. cit.* p. 246.

NOTES ON THE PROGRESS OF MENDELIAN STUDIES

[*Reports to the Evolution Committee of the Royal Society*, II, 1905, pp. 119–131]

DURING the two years that have passed since the publication of Report I the growth of Mendelian literature has been so rapid that it is impossible to give any adequate summary here. We can only specify the more significant results of recent work.

New Mendelian Cases. The valuable memoir of Coutagne[1] on heredity in the silkworm, written without a knowledge of Mendel, shows that several of the characters studied have a Mendelian inheritance. Of the larval characters both black colour and transverse striping are evidently dominants to the normal whitish colour. In most of the cases white silk is dominant to yellow silk, one race presenting an exception to this rule. An artificial race of dark moths also showed a partial dominance (with some blending) over the normal light colour. This dark race was made by the use of two dark males which seem to have arisen as a sport. These were bred (1889) with the brownest females which could be found in a normal race, and from the offspring a dark race was produced by selection in about five years.

In the case of each of these characters the gametic segregation was evidently complete or almost complete, and the purity of the recessives at least was established in numerous experiments. Apart from cases of mixture of *DR* and *DD*, some irregularities are noticeable, but the general course of the inheritance is quite clear. Three larvæ were seen which were black on one side and white on the other, an important phenomenon occasionally seen in discontinuous variations of *Lepidoptera*, comparable, no doubt, with gynandromorphism.

In contrast with Mendelian inheritance of these discontinuous characters, the character, called by Coutagne *richesse de soie*, shows, to all appearances, continuous variation and a non-Mendelian inheritance, not undergoing any sharp gametic segregation, and being capable of intensification by gradual selection. It is likely that this quality depends on numerous factors[2].

[1] "L'hérédité chez les Vers à Soie," *Bull. Sci., Fr. et Belg.* XXXVII, 1902.

[2] Coutagne's memoir contains very many facts of great importance which cannot be referred to here. The attention of students of evolution is also called to the same author's "Recherches sur le Polymorphisme des Mollusques de France," *Soc. Agric. Sc. Ind. de Lyon*, 1895, a treatise of altogether exceptional value on the interrelations of varieties and the significance of locality.

A peculiar case of recessive variety, generally female, has been pointed out by Doncaster[1] in the case of *Abraxas grossulariata* var. *lacticolor* on the experimental evidence obtained by G. H. Raynor.

From the records of former experimenters there could be little doubt that the long-styled form in *Primula* is recessive to the short-styled, and experiments in progress (begun by W. Bateson in conjunction with R. P. Gregory) have confirmed this view. It is, however, doubtful as yet whether any *pure* short-styled plants exist, F_1 being a mixture of longs and shorts, of which the longs breed true. Whether the mixture is due to heterozygosis in the thrums used, or to a perpetual production of long-style gametes as a *Halb-rasse* by the short-styled plants, is not quite certain[2]. Horticulturists have decreed that the pin-eye is the correct form of *P. sinensis*, but all Auriculas and Polyanthuses must be thrums. Owing to the recessive nature of the long style, the short style has been totally eliminated from most English collections of *sinensis*, and now is only to be procured with difficulty. But there is apparently no *Auricula* or *Polyanthus* which breeds true to thrum eye, though such strains would certainly be in demand. Hence we are led to infer that the persistent appearance of the pin-eye is due to a perpetual output of recessive gametes by the thrums (see later paragraph on Sex, p. 131). The homostyled type which is also characterised by a great extension of the yellow centre or eye is recessive to both long and short style. For continued opportunities of studying the breeding of *P. sinensis* at Reading we are greatly indebted to Messrs Sutton and Sons. A detailed account of these observations will be prepared later. Further observation has confirmed the statement in Report I that the fern-leaved type is recessive to the palm-leaved, segregating from it perfectly, with very rare exceptions. The green stem is similarly recessive to reddish stem, but the deep red stem is also recessive to the reddish. The curious form known as "ivy-leaved" is also a recessive to palmate leaf, segregating perfectly from it. *Double* flowers constitute a recessive character, as in Stocks (see R. p. 33)[3].

As regards colour inheritance there are some complications not fully explored. Pure white on a green stem is almost certainly recessive to all colours, but the white strains on coloured stems may

[1] *Ent. Rec.* xv, 1903, p. 142.

[2] From the later evidence there is little doubt that pure short-styled plants exist. February, 1905.

sometimes give white F_1, even when the other parent is a fully coloured type. On this point the evidence is not altogether consistent, and more inquiry is needed. It is possible that the presence or absence of colour in the stem affects the result.

Blue may be almost entirely broken up on crossing, rarely reappearing in F_2, probably as 1 in 16.

The case of certain pink-flaked and mauve-flaked types is of more practical importance. The pink is recessive and breeds true at once. The mauves, on the other hand, may throw pinks. Savings from individual plants showed that some are pure or *DD* mauves and others are heterozygotes of mauve and pink. A pure strain of mauves may be immediately obtained by saving from a homozygous mauve.

The work of Biffen has greatly extended the application of Mendelian principles in the case of wheat (see *Journ. Agri. Sci.* I).

Castle[1] has found the rough, "rosetted" or "Abyssinian" condition of the coat in guinea-pigs dominant over the normal smooth coat, and that the Angora coat is recessive to the normal in both rabbits and guinea-pigs.

We are indebted to Mrs Staples-Browne, of Bampton, for a game Bantam cock and two hens bred from ♀ brown-red × ♂ black-red, both believed to be pure. All three are very near the brown-red in colour. The two hens have the purple or "gipsy" face of the brown-red, almost, if not quite as well developed as pure brown-reds. The cock's face, though showing a tinge of purple, is more nearly the ordinary red. This dominance of so novel a character as brown-red and purple face is somewhat exceptional. In their down the F_1 chicks are said to have been very dark, thus also resembling the brown breasted.

The paper just published by A. Lang contains evidence, which as the author states, goes far to show that the well-known discontinuity between the banded and bandless *Helix hortensis* depends on Mendelian segregation[2]. The bandless character is dominant.

The poultry cases here related illustrate the simultaneous segregation of *four* allelomorphic comb-characters.

Biffen (*loc. cit.*) has found *primâ facie* evidence for the belief that in wheat, power of resisting rust is a recessive character. The remarkable case referred to by Orton[3] in cotton seems rather to indicate that resistance to the wilt disease is a dominant character.

[1] *Science*, N.S. XVIII, 1903.
[2] *Festsch. z. Siebzigsten Geburtstage v. E. Haeckel*, 1904, pp. 482, 503.
[3] *U.S. Dep. of Agric. Bull.* No. 27, 1900.

Reversion. When F_1 presents a character distinct from that of either parent, it is not rarely reversionary. In addition to the cases hitherto noticed, an interesting one was exhibited by Hurst at the Southport Meeting of the British Association, white Angora rabbit × Belgian hare giving F_1 grey like a wild rabbit. These experiments are in progress and will be published hereafter.

The cases given above respecting Sweet Peas are of a somewhat distinct type, as in them two entirely white or "albino" plants gave a coloured reversion, which in some families was complete, to the wild purple type, and in other families took the form of "half-reversion" to the red bicolour "Painted Lady" type. This is a well-known and ancient type of the cultivated flower, said to occur wild in Sicily.

The appearance of hoary F_1 as the result of crossing certain glabrous Stocks is one of the few examples of reversion in a "structural" character as distinguished from colour (see later, p. 127).

Special interest attaches to the behaviour of yellow flowers in their crosses. It is to be remembered that yellow may be due to various physiological types of pigmentation, and the evidence is complicated by the frequent occurrence of reversion in F_1. Cream Stocks and white, for instance, give purple F_1. Cream Sweet Peas may do the same. Correns[1] found that in *Mirabilis jalapa* yellow and white always gives red. The evidence from generations of Sweet Peas and Stocks later than F_2 plainly shows that there may also be simple dominance of *white*, viz. no *coloured* plastids, over cream, or coloured plastids. Correns states that in his *Mirabilis* F_1 there was no trace of yellow (except a spot in a mosaic). Mr Lynch has called our attention to the case of *Begonia Weltonensis* (pink), from *B. Sutherlandi* (orange), and *B. Dregei* (white), which is perhaps comparable. Before the relations of these dissimilar illustrations can be compared, the nature of the yellow in each case must be determined. In the Begonia case it is not impossible that the pink of the hybrid is due to dominance of the sap-colour from *Sutherlandi* while its chromoplastic yellow is recessive.

Monolepsis. In considering this subject (Report I, p. 155)[2], we were not aware that a suggestion very similar to our own had been proposed by Giard[3]. Further information respecting Orchid cases was

[1] *Ber. Deut. Bot. Ges.* xx, 1903, p. 605.

[2] [This volume, p. 62.]

[3] See especially Giard, *C.R. Soc. Biol.* LV, 1903, p. 779, and *Cinquantenaire Soc. Biol.* p. 12.

given by Hurst[1]. In connection with Millardet's original observation on the Strawberry, a record of Andrew Knight[2] respecting a case in the Strawberry, possibly of a similar nature, is interesting. Further information as to the phenomenon is greatly to be desired, and it is unfortunate that the recorded cases relate to subjects which for various reasons are difficult to experiment with.

Mixture of forms in F_1. In certain cases two types which each breed true separately, give, on crossing, individuals of two or more kinds. If this complication is not determined by sexual dimorphism, one or other of the two pure types must, in reality, be giving off more than one type of gamete. There are then two possibilities only. Either the difference between these types of gamete lies in the characters with which they are endowed in gametogenesis, or in the manner in which they are affected by fertilisation. In the former case we must conceive of the gametes of the parental type A being, in reality, xA and yA; in the latter they may be called xyA, but on fertilisation with some other pure type there is a partial monolepsis, by which on fertilisation with B, sometimes the result is xAB, and sometimes yAB, and not always $xyAB$. Up to the present time there is no case which can be positively declared to be of the latter class, but as monolepsis certainly occurs in the complete form, the possibility of partial monolepsis should not be forgotten. For a long time it seemed that the phenomena seen in Malay crosses must point to this interpretation, but further experience is not favourable to that suggestion.

In most of the recorded instances of mixed F_1 there is now no doubt that the first is the true account. In discussing the results of Crampe attention was called[3] to the possibility that the dissimilarity between two F_1 forms from "pure" parents might turn on a hidden distinction *either* between the different albinos, *or* between the different coloured parents, and that in certain cases of Parsons the distinction was certainly in the albinos, most giving pied offspring while self-coloured F_1 came from others.

At this point the recent paper of Cuénot[4] marks a very important advance. Mixed F_1 has been several times recorded in mice, some families containing blacks and greys, though the parents in each case seemed to be pure. It had appeared to us that here the probable

[1] *Gard. Chron.* II, 1903, p. 227.
[2] *Trans. Hort. Soc.* v, 1824, p. 294.
[3] W. Bateson, *Proc. Zool. Soc.* II, 1903, pp. 78 and 84. [This vol. pp. 84 and 90.]
[4] Cuénot, *Arch. Zool. exp. et gén., Notes et Rev.* XI, 1904, pp. 45 to 56.

interpretation lay in impurity of the coloured parents, but Cuénot has now proved that albinos extracted from the several colours will give those colours on crossing with coloured types.

Still more significant is his proof that by crossing albinos of different *extraction the allelomorphs determining the various colours will themselves segregate* in the gametogenesis of the albino in ordinary Mendelian fashion. For example, albino *ex* yellow bred with albino *ex* black gives a heterozygous albino whose gametes are in equal numbers bearers of the factors which determine to black or to yellow respectively. When such an albino breeds with a pure colour-type, a mixed F_1 may result. As he points out, this fact disposes of various outstanding difficulties met with by Darbishire and others. The appearance of the two reversion types in Sweet Pea is almost certainly determined by similar factors, though the proof can only appear next season.

[*Note added December,* 1904

Tschermak[1] had previously brought forward a large mass of facts of a similar nature, and (in view of Cuénot's evidence) his account is clearly correct, applying perhaps to all cases where F_2 gives the ratio $9 : 3 : 3 + 1$. It is, however, doubtful whether we should speak of such factors as "latent." It is rather that an element is present which when it meets another element produces a certain character in the fertilised result. This is not the character which was latent. As stated later, there is still a case, that of hoariness resulting from the crossing of glabrous Stocks, to which no adaptation of this simple view is yet applicable.]

Peculiarities of Extracted Types. In addition to the fact observed by Cuénot that an extracted type (*e.g.* albino) may carry on segregable determinants, whereby the individuals may, in reality, differ from each other, though outwardly alike, there are other specific properties of extracted types which call for notice. At an early stage in the inquiry it was remarked that though gametic unions between certain pure types give reversion, unions between extracted gametes, ostensibly similar to the pure ones, give no reversion. This has now been seen most clearly in Sweet Peas where, so far, two dissimilar recessives (long white × round white) of the same extraction, crossed together, give no reversion, though the plants used are indistinguishable from the two original types which gave the reversion. Moreover

[1] *Beihefte zum Bot. Cblt.* XVI, 1903, Heft 1.

in Stocks when one such extracted is crossed with one of the *original* pure types, there is no reversion, though a *new* pure type may cause the reversion again. Conversely, in Stocks, $DR_1 \times DR_2$, where D is a white hoary, may give some glabrous, while $DR_1 \times DR_3$ give only hoary.

These phenomena must be distinguished from that described by Cuénot; for in the cases now under consideration the quality which determines or prevents the reversion is apparently common to all the sister cross-breds and does not depend on any segregable or allelomorphic character. Therefore, though the process, so far as we yet know is quite specific in its results, it is not Mendelian. In view of these facts the nature of the reversionary forms in F_2 is often problematical. The relation of the two phenomena is a question which only the later generations can solve.

With the facts just described may he compared the results obtained in Stocks, where among the glabrous types, not only white × red, and cream × red give reversion to hoary, but the same reversion occurs when white is crossed with cream. Therefore, the reversion cannot be regarded as merely due to the meeting of a pair of elements, of which one is borne by each type, but it must have some more complex causation.

Resolution and Disintegration: Synthesis. The conception of resolution applies properly only to those cases where a character appearing in F_2 is constituted by the breaking up of the compound allelomorphs of the original parents, the term disintegration being reserved for cases when the integrity of an allelomorph is impaired and segregation is incomplete. Thus the occurrence of homozygous types in F_2 made as a blending or mosaic of the original parental allelomorphs is an indication of disintegration. For instance, the white-spangled types seen in F_2 from Brown Leghorn × white, and certain chequered types, similarly produced, must be regarded as acquiring their colour from the coloured parent, and their white from the white parent, which is then disintegrated.

In view of Cuénot's evidence great care will be needed in discriminating these various cases. The uniformity of F_1 will generally be a guide to the nature of the case, but at least the homozygous nature of the F_2 type in question must be tested in each instance. It is not inconceivable that, owing to dominance and other peculiarities of heterozygosis, F_1 may be uniform though the gametes of one or other parent are not so, and a spurious appearance of resolution may

thus appear in F_2. In such cases sensible uniformity in the statistical composition of F_2, together with proof of homozygosis of resolved forms, will furnish the only reliable criterion as to real resolution in F_1.

It should be especially noted that the phenomenon detected by Cuénot, while simplifying some cases, formerly interpreted as resolution, does not provide a substitute for that conception; for, to go no further, we still have to deal with cases where one of the original pure types practically disappears from F_2, etc., having evidently been entirely or almost entirely broken up in the gametogenesis of F_1 (*e.g.* blue flower-colour in *Primula sinensis* (p. 123), the red of some Sweet Peas (R. p. 90)).

As to the statistical relations of the products of resolution there is, as yet, no evidence which is quite satisfactory, and it is clear that several types of cases occur. The case of *Antirrhinum* studied by de Vries[1] seems to be peculiar in the fact that, on crossing red × white only 1 white in 16 appeared in F_2[2].

An intensification of one of the pure parental characters is not rare in some members of F_2 where resolution occurs. Perhaps the most striking illustration is that seen by Biffen (*loc. cit.* p. 31) in the case of lax ear in Wheat. A similar case in colour is given on p. 90 of this Report.

Tschermak's[3] cases of resolution in *Matthiola* are, thus far, the most fully studied, F_3 having been already reached. They give valuable indications as to the statistical relations in a case where resolution follows on reversion in F_1; though, for this reason, the precise interpretation of the phenomena is somewhat obscure.

All the available facts support the expectation that a symmetry will be found to prevail in the distribution of the resolved characters comparable with that occurring in the case of unresolved characters in ordinary mono-hybrids.

It is desirable that the term synthesis should be restricted in heredity to the permanent union of component allelomorphs to form a compound allelomorph which breeds true without segregation. Such

[1] *Mutationstheorie*, II, p. 198.

[2] [*Note added December*, 1904—In *Camb. Phil. Soc. Proc.* XII, p. 50, I suggested that this result might be attained if F_1 produced 4 types of gametes in equal numbers. Mr R. H. Lock has pointed out to me that the case may very probably be regarded as an *actual* example of "di-hybridism." If this proves to be true there is then no resolution or synthesis to be reckoned with, and the original red would not be, gametically, a compound character.—W.B.]

[3] *Beihefte z. Bot. Cbltt.* XVI, 1903, p. 18.

an example is seen in the case of the "walnut" (*rp*) comb, produced by crossing rose-comb with pea-comb. The F_1 comb, thus artificially formed, may be scarcely, if at all, distinguishable from the natural "walnut" comb of the Malay breed. F_1 produces four types of gametes (probably in equal numbers), *rp*, *r*, *p*, *s*. Among the F_2 types there are, therefore, some birds formed by $rp \times rp$, and the evidence (1904) proves that some, at least, of these are then really synthetic *rp*, breeding true to that character.

Tschermak's discovery that after the production of reversionary purple F_1 in *Matthiola*, certain purples appear in F_2 which seem capable of breeding true, probably points to a similar permanent synthesis[1]. Here, however, a complex resolution has evidently taken place, and possibly these cases may prove to be analogous with the production of various homozygotes after resolution; for the degree to which the compound allelomorphs of the new forms derive elements from both pure types is not yet determined.

Heterozygous Breeds. As an illustration of a breed permanently heterozygous, the Andalusian fowl was given tentatively in Report I. Experiments have now shown that this is the true account. The blue Andalusian gives off gametes, black and white-splashed. The blue is formed by heterozygosis of these two, but the black and the white-splashed birds, produced by mating blues together, are homozygous and generally breed true. Further study of the Giant Lavender, *Primula sinensis*[2], has confirmed the view that this also is a heterozygote of magenta and white-tinged, offering an exact parallel to the Andalusian. In each case there is, however, a doubt as to whether the white-splashed or tinged may not, in certain cases, subsequently segregate into a purer white and a form more distinctly coloured, possibilities which require further investigation.

Sex. In Report I we indicated the possibility that sex may be ultimately a phenomenon of gametic segregation comparable with

[1] [*Note added December*, 1904.—Our later results with Sweet Peas prove that there also a synthesis has occurred, forming purple-bearing gametes, and bicolour-bearing gametes. A strain of pure purple and of pure bicolours can thus be produced from F_2 made by white × white. The same is true for the picotee and tinged white types in F_2.

Darbishire's results (*Biometrika*, III, Pt I, pp. 24, 25) are without doubt capable of a similar explanation. Some of the greys in F_2 and later generations are evidently in composition grey × grey or some other colour. The deficiency of albinos in the matings where such greys were used is therefore in harmony with the facts seen in Sweet Peas, Stocks, etc., as must appear at once when the offspring of each individual are made separately traceable in the Tables.]

[2] W. Bateson, *Mendel's Principles of Heredity*, 1902, p. 182.

that seen in ordinary Mendelian cases. In an interesting essay, Castle[1] has greatly amplified this suggestion, and has shown reasons for believing that the segregation of male spermatozoon from female spermatozoon and of male ovum from female ovum may occur at the reduction-division in gametogenesis. While admitting the likelihood of this suggestion, we feel that for the present it should be received with caution. In particular, we doubt the conclusion that *both* ova and spermatozoa (after a reduction-division) are always bearers of either the male or the female character. It seems more likely that special cases will present special phenomena in this respect. As yet the evidence most applicable to the decision of the question is thus derived from those reciprocal crosses which give dissimilar results, and in view of the idiosyncrasies of these cases, we incline to expect that sometimes the male element, sometimes the female, will be found to be responsible for sexual differentiation, and that the similar differentiation of both elements is not likely to be universal. For instance, if the case of Malays, already discussed (R. p. 111), be shown to bear the suggested interpretation, it is evident that the gametes of one sex alone, probably the male, and not both, will determine the sex of the offspring. One sex must then be regarded as a "Halbrasse" of the other, just as long style may, perhaps, be of short style in *Primula*.

The evidence of Correns[2] as to Bryony crosses has a direct bearing on this question. Using *Bryonia alba* ♀ as seed-plant and *B. dioica* as male, he obtained offspring all diœcious (with a doubtful exception). As he states, this fact points to the segregation of the sex-determinants among the male cells of *Bryonia*. The result of the reciprocal cross will be awaited with interest.

Gärtner[3], however, using ♀ *Lychnis diurna* × ♂ *L. flos cuculi* (♀) also obtained F_1 all diœcious, males and females, pointing to sex-segregation among the egg cells of the mother. In each of these cases, unfortunately, the problem is complicated by the appearance of sterility in F_1, and in the case of ♀ *L. diurna* × ♂ *Silene noctiflora* (♀) the results were somewhat ambiguous[4].

A case that may be used for the elucidation of this problem is that of the Cinnamon Canary, recently described by Norduijn[5], who has

[1] *Bull. Harvard Mus.* XL, 1903.
[2] *Ber. Deut. Bot. Ges.* XXI, 1903, p. 195.
[3] *Bastarderzeugung*, p. 49.
[4] *Ibid.* p. 287.
[5] *Album der Natuur*, 1903, p. 71. See also Blakiston, Swaysland, and Wiener, *The Canary Book*; Jerome, *Canary Breeding*, 1896, etc.

most kindly given us much supplementary information. As to the essential facts, Canary-breeders seem to be agreed. The Canary has two forms which are both in a sense albinos, the yellow and the cinnamon. The latter, in the nestling stage at least, has red eyes, which subsequently darken, but red eyes may occur also in yellows. When green (viz. non-albino) ♀'s are crossed with cinnamon ♂'s, both greens and cinnamons are produced, of which the males are always and the females sometimes green, but *the cinnamons are invariably female*. From the reciprocal cross the young are always green.

The F_1 males from cinnamon ♂, when bred with green or yellow ♀'s, may again produce cinnamons which are exclusively ♀. The interpretation of this case is still quite obscure, but attention is called to it as a most important subject of experiment. The facts strongly suggest that there is here some phenomenon of gametic coupling[1] of the female sex-character with cinnamon. When yellows are used the results are complicated by the appearance of reversionary hetero zygotes, green or green-marked.

Castle is doubtless right in the view that marked inequalities observed in the distribution of characters between the sexes after crossing are due to some similar coupling of a sex-character with some allelomorphs[2], and the investigation of these cases will probably much elucidate the real nature of sexual differentiation. The phenomenon of sex is possibly comparable in some aspects with that of the "*Mittelrassen*" of de Vries, the production of one form being, in gametogenesis, constantly accompanied by the production of a second.

In the sweet peas with sterile anthers we have a phenomenon which may be described by a slight stretch of language as Mendelian segregation of a female from a hermaphrodite (see R. p. 91).

Disturbances, due to sex, have been met with by several observers, a particularly striking one being recorded by Hurst (R. p. 148).

The Moment of Segregation. The balance of evidence is in favour of the belief that gametic segregation takes place at the reduction-

[1] In Report I, we took exception to Correns' use of the term "conjugation" to denote this association of characters, preferring the word "correlation" already in use. Experience, however, has shown that, owing to the special uses of correlation now prevalent, the term here leads to confusion. No such objection attaches to the words "coupling" or "coupled," also introduced by Correns in the same sense, which in future we propose to adopt.

[2] For a case of a curious distribution of such varieties in a wild form, see the case of the beetle, *Gonioctena variabilis*, W. Bateson, *Proc. Zool. Soc.* 1895, p. 850.

division, but no crucial test is yet forthcoming. The new evidence as to the individuality of the chromosomes and the discovery that a true transverse division occurs in the chromosomes of plants at reduction are clearly favourable to the hypothesis that the reduction-division is the critical moment. A fact which rather suggests that segregation occurs at some earlier dichotomy, is the irregularity of the individual F_2 ratios (cf. R. pp. 88 and 108) in certain cases (*e.g.* Poultry), which strongly contrast with the extreme regularity of these ratios in the case of wheat, for example (Biffen), or maize (Lock).

Up to the present time the attempt to discover an order in the occurrence of the gametes, bearing either of a pair of allelomorphs, has led to negative results. The case of *Pisum* seemed not unpromising for this inquiry, but a considerable number of pollinations of *DR* plants with *R* pollen has, so far, failed to show that the *D* and *R* ovules are arranged in any definite pattern or order, but as conceivably more than one plant[1] may have to be taken into account, the recognition of the arrangement may be a very difficult matter.

As to the factors which determine the retention or exclusion of any character in the case of any germ cell, no suggestion has yet been made. *It is not impossible that this may be influenced by some factor* easily disturbed by environmental influences, so far, at least, as the egg cell is concerned. To take a crude illustration, if gravitation effected the result, the regularity of the order might be obliterated by the action of the wind at the moment of segregation. Improbable as this particular suggestion obviously is, it is, perhaps, to some irregularity of a similar nature that the want of a visible order may be due.

The relation of *gametic* differentiation to the normal differentiation between *somatic* parts of the same body is one which, sooner or later, will call for consideration. There are besides many examples of differentiation between somatic organs manifesting itself in bud-sports, where the differentiating pair of characters are such as we elsewhere know to be an allelomorphic pair.

Statistical Consequences of Mendelian Heredity. This subject has been discussed by Yule[2] and by Pearson[3]. In Report I, p. 158[4], we

[1] For example, there is every likelihood that the seeds from the right and left carpellary edges are antidromic, though all stigmas turn to the flower's right (see Macloskie, *Am. Nat.* November, 1895).

[2] *New Phytologist*, I, 1902.

[3] *Phil. Trans.* 1904, 203 A, p. 53, and *Roy. Soc. Proc.* LXXIII, 1904, p. 262.

[4] [See this volume, p. 66.]

suggested "that Galton's law may be a representation of particular groups of cases which are, in fact, Mendelian," in the sense that the gametes are pure. The analysis carried out by Yule points to a similar conclusion, if the phenomena of dominance and special consequences of heterozygosis are neglected. Pearson's conclusion that various phenomena of inheritance studied by him are incompatible with Mendelian expectation is open to the objection that many of his characters are obviously liable to such great disturbances from the interference of conditions that the operations of heredity alone must be largely obliterated. In other classes of cases to which he refers (various colour phenomena) no sufficient analysis is yet provided, and in such a field comprehensive statistics are an inadequate indication as to the underlying physiological processes.

The experiments of Johannsen[1] have made an important contribution to this part of the inquiry. Taking self-fertilised beans (*Phaseolus*) he found indications that the number of "pure lines" in respect of seed-weight was very considerable. Hence we may suppose with some confidence that segregation, in respect of this character, deals with units which, though small, have a sensible size. It is to be hoped that others will be attracted to this fruitful method of research.

General. As the results of experiments now in progress here and elsewhere will soon clear up many doubtful points, we propose to defer a general survey of the subject. Certain conclusions of significance are, nevertheless, obvious.

The solution of the various problems of heredity is now seen to depend primarily on a study of the process of segregation in gametogenesis, and secondarily on a determination of the specific consequences of the union of gametes of the various types in fertilisation. These questions can be answered only by a minute experimental analysis, and little advance can be expected from study of the phenomena in the mass by comprehensive statistical methods, however appropriate such treatment may have seemed in the absence of any knowledge of the physiological processes which constitute heredity.

In a large and rapidly increasing number of cases, it is known that segregation of characters is sensibly complete, the characters being thus allelomorphic and the gametes bearing them pure. Such allelomorphism may apparently subsist in the case of any character of animals or plants. Though naturally the phenomenon is more easily demonstrated for some characters than others, any one who conducts

[1] *Erblichkeit in Populationen*, Jena, 1903.

breeding experiments can perceive frequent indications of the prevalence of segregation in numberless dissimilar characters.

In fowls, for instance, there is no reasonable doubt that such features as late or early feathering, shortness of wing-quills and tail, *peculiar qualities of voice, forms of constitutional weakness, follow* rules closely similar to those detected in features more amenable to critical study. There is no reason to suppose that physiological distinctions, such as liability to disease (cf. p. 123, and Biffen, *loc. cit.* p. 40), late and early ripening (Biffen, p. 34), certain forms of sterility (see R. p. 91), and so forth, will be exempt from the operation of these rules. There are already indications, moreover, that such features may be gametically coupled with others more easy to deal with, for example, certain types of pigmentation.

On the other hand, it has been asserted that certain experiments have demonstrated that gametic purity does not occur in cases where its presence might be expected, *e.g.* the colours of mice[1]. It appears to us, however, that the analysis of these cases is as yet materially imperfect. The evidence in the case of *Matthiola*, for instance, shows that many complexities have to be considered before such negative propositions can be established.

Especially in dealing with extracted types caution is needed. Difference between the behaviour of an extracted and an originally pure type may evidently be caused by the presence of various determining characters, which though imperceptible until a cross is made, may modify the result. Nevertheless, these hidden characters may themselves be allelomorphic to each other in a simple Mendelian fashion (Cuénot), and the phenomena may illustrate gametic purity in the strictest sense.

Irregularities resulting from the direct action of conditions may also obscure the simplicity of the result, and mistakes of interpretation may easily occur through want of attention to this fact (cf. Peas, R. pp. 58 and 64).

[1] Darbishire, *Biometrika*, III, p. 1, *passim.*

A SUGGESTION AS TO THE NATURE OF THE "WALNUT" COMB IN FOWLS

[*Proceedings of the Cambridge Philosophical Society*, XIII, 1905]

In Report II to the Evolution Committee of the Roy. Soc. p. 109, we discussed the problem of Malay or "walnut" combs in fowls on the supposition that the four types of comb, viz. single (*s*), pea (*p*), rose (*r*), and "walnut" (*rp*), are allelomorphic to each other.

The facts are (1) that $r \times p$ gives in F_1 a zygotic combination *rp*, which differs in essential features from any other kind of comb, especially in the presence of feathers or hairs on its surface usually disposed as a transverse band.

(2) That the gametes of this F_1 are of four types, *s*, *r*, *p*, *rp*, in equal numbers, which is proved by the result of breeding the F_1 with a single. Similarly $F_1 \times F_1$ gives an average of 9*rp*, 3*r*, 3*p*, 1*s*.

(3) The *rp* birds in F_2 may then be pure *rp*; or they may give off only *r* and *rp*; or only *p* and *rp*; or again they may bear gametes of all four types. We have thus far failed to find any individuals that give only *rp* and *s*; or to distinguish any class as the product of $rp \times s$ from those which are the product of $r \times p$.

The *rp* gametes were regarded as true examples of gametic synthesis, and the appearance of *s*, absent from both pure parents, was treated as due to a resolution or break-up of either the *r*, the *p*, or both. A much simpler and probably more correct account has since suggested itself, which it is the object of this note to consider.

This suggestion will be made more intelligible by describing the way in which it was reached. Certain experiments on *Primula sinensis* made by R. P. Gregory in conjunction with W. Bateson[1] had shown that short style, or thrum, is dominant to long style, or pin. In addition to these two types a condition is known which, following Darwin, we have called *homostyle*. In it the anthers are at the level proper to pin, but the style does not pass through them, and the stigma is at the level of the anthers, the whole style having the length proper to the thrum type. The pollen of homostyles is of the pin type. The corollas, however, are peculiar in that they always have a yellow flush which extends the "eye" far up the petals (whence the best known homostyle strain derives the name of "Primrose Queen").

In the course of the work thrum was crossed with homostyle, giving

[1] [See this volume, pp. 115–120. Ed.]

F_1 ordinary thrum without the yellow flush. But F_2 consisted of four types: (1) thrum without yellow flush; (2) thrum with yellow flush; (3) *pin* without yellow flush; (4) homostyles with yellow flush. The ratios were evidently 9 : 3 : 3 : 1. The form pin, not introduced as an original parent, thus appears in F_2 as a novelty.

The interpretation is obvious. The allelomorphic pairs are clearly two. (1) Thrum (*D*) and pin (*R*). (2) No yellow flush (*D*) and yellow flush (*R*); and the homostyle is merely a zygotic state occurring when yellow flush and pin coincide. The pin therefore appears as a novelty by the meeting of pin and "no yellow flush."

This observation naturally suggested that the single comb in F_2 from $r \times p$ might have a similar mode of origin. Applying this hypothesis the original parents, *r* and *p*, are regarded as respectively rose + no-pea, and pea + no-rose. The allelomorphs are (1) rose and absence of rose; (2) pea and absence of pea. The rose and the pea characters belong to distinct allelomorphic pairs. When therefore *r* meets *p* the zygote would be walnut, and the *single* is regarded as constituted by the meeting of gametes bearing neither rose nor pea. In this way all the phenomena are brought into simple relation with each other and the case is exactly comparable with that of any other dihybrid. This suggestion has the merit that it obviates any appeal to resolution, and that the gametic synthesis apparently occurring in the case of the *rp* character becomes an ordinary phenomenon of dihybrid inheritance. Finally, the fact that $r \times p$ cannot be distinguished from $rp \times s$ finds a ready explanation.

If we do not look beyond the special case of the walnut combs, this account seems so complete as to make further discussion unnecessary. We can only express surprise at our failure to perceive it sooner. This failure was of course due to the preconception that the types of comb were definite entities alternative to each other, while, as is now evident, the *presence* of a given modification must be regarded as allelomorphic to the *absence* of the same modification. The essential feature of the rose comb is its papillosity, while the ridges mark the pea. The single comb is thus to be regarded as a comb into which no such additional element is introduced, being neither papillose nor ridged, and is thus a factor common to all the other types, rose, pea, and walnut.

Previously we had regarded the allelomorphism as existing between the various factors which caused the comb to be either rose, pea, walnut, or single. The critical point of difference between the

two views lies in the way in which single is regarded. While formerly we treated it as a positive condition segregating from the others, on what we may call the presence-and-absence hypothesis it is to be recognised as the original state into which the factor—or pangen, if we use de Vries' term—for rose, pea, etc., has been introduced.

Since the ratios, both of characters and hereditary powers, are identical in both cases, simple experiment does not discriminate between the two possibilities; though certainly if all the different kinds of elaborated combs[1], such as Houdan, Crève-Cœur, etc., are found to give singles in F_2 from rose or pea, the fact will tell distinctly in favour of the presence-and-absence hypothesis.

In spite of the great simplification which this conception effects, there are certain difficulties besetting it. In the first place it is not readily conceivable that rose and pea are in reality nothing but rose elements on a basis of single comb, or pea elements on a basis of single comb. This difficulty is especially great in the case of the Indian Game hen and the Malay hen, for in each of these the comb is so low that it can scarcely be regarded as formed merely by the moulding of even a low single comb into the pea or walnut shape. An extreme difficulty of a similar kind is presented by the fact that the walnut comb has special characteristics not present in either rose or pea, notably the hairs or feathers on its surface. We must recognise, therefore, that if these forms are produced by the addition of shape-elements such as rose, or pea, or both, the result is not merely that which would be expected as the consequence of simple additions.

If we take a somewhat wider range and consider the possibility of applying such presence-and-absence hypotheses to the phenomena of heredity at large further difficulties are encountered, to which it may be well to make reference now. For example, the phenomenon of dominance on the part of a *negative* character is difficult to reconcile with this conception. Such a case occurs even in the combs, for the Fowl × Pheasant is declared to be always without any comb at all[2]. Striking cases have been recorded by Biffen[3] in Barley crosses, where the absence of female organs in the lateral florets, and even absence of the lateral florets altogether, was found to be dominant

[1] Mr C. C. Hurst has suggested to us that a particularly interesting experiment on this point could be made by crossing the Breda fowl with rose or pea. The Breda is described as having *no* comb, but a concavity in its place. In it the wattles are represented as of the size proper to an ordinary single-combed fowl.

[2] See for instance Tegetmeier, *The Poultry Book*, 1867, p. 165.

[3] Biffen, R. H., *Journ. Agric. Sci.* I, 1905, p. 255.

over the presence of fully developed flowers. Doubtless the statement could be inverted, and it could be suggested that the absence of the florets, etc. was due to the *presence* of some element which prevented their growth, but that would be to abandon all judgments based on the actual appearances, and the terms would become meaningless.

The next question is whether hypotheses of presence-and-absence provide a substitute for the conception of compound allelomorphs. In many cases it is likely that characters at first sight reckoned as compound will prove to be made up, like the walnut comb, by the co-existence in one zygote of elements belonging to distinct allelomorphic pairs.

For instance, the colour of a flower, made up of both sap-elements and plastid-elements, might pass for a compound character. Here a disproof is easily obtained from the fact that such a flower when crossed with white will give in F_2 the four types, sap-colour alone, sap-colour + plastid-colour, white alone, plastid-colour alone. Conversely a red crossed with cream (viz. plastid-colour) will give some whites in F_2, as in Sweet Peas and Stocks[1]. But that there are limits to the extension of this principle is suggested, *e.g.* by the class of cases in which F_2 contains a number of new types, though one of the original pure types may not reappear. Such a case is that of Brown Leghorn × White Leghorn, which gives in F_2 cuckoo, slaty, pile, etc., but the Brown Leghorn colour has not reappeared in about 500 chicks.

Other cases with which any hypothesis of the mere presence and absence of characters cannot apparently deal are to be found among the phenomena of reversion and the peculiarities seen in the behaviour of extracted types; but until the evidence on this part of the subject is more complete it can scarcely be profitably discussed.

[1] *Roy. Soc. Evol. Com. Rep.* II, 1905, pp. 27 and 86.

FURTHER EXPERIMENTS ON INHERITANCE IN SWEET PEAS AND STOCKS: PRELIMINARY ACCOUNT

[*Proceedings of the Royal Society*, B. LXXVII, 1905]

LATER results have provided expressions which include many of the peculiar phenomena of inheritance already witnessed in Sweet Peas and Stocks. In Sweet Peas we have shown that purple may occur, as a "reversion," from the cross between two whites, one having long pollen grains, the other round. Similarly in Stocks, white glabrous × cream glabrous gives "reversionary" F_1 purple hoary. (In both cases the parents are whites, *i.e.* free from sap colour, for cream is due to yellow plastids, recessive to colourless plastids.)

The appearance of coloured flowers is due to the simultaneous presence in the zygote of two factors, belonging to distinct allelomorphic pairs, which may be spoken of as C, c, and R, r, the large letter denoting presence, the small letter the absence of the particular factor.

Hoariness of Stocks is similarly due to the co-existence of two other factors, and the presence of either of these factors is also allelomorphic to its absence. Tbese two pairs are spoken of as H, h, and K, k. But, though H and K may both be present, no hoariness is produced unless C and R, the colour factors, are also both present. For the actual development of hoariness four factors are thus required. The existence of white-flowered hoary plants creates a difficulty; but white *incana* is evidently a coloured form in reality, for its flowers tinge on fading, and its embryo has the deep green colour characteristic of purple varieties. Apart from breeding tests, however, white hoary *Bromptons* show no visible indication of colour, and as yet they constitute a marked exception.

White glabrous and cream glabrous types contain both H and K, the two elements of hoariness. One of them contains C and the other contains R. All sap coloured types studied contain one only of the two factors H, K. Consequently, we find tbe following result, which formerly seemed paradoxical:

			F_1
1.	Cream glabrous	× Red or purple glabrous	Red or purple hoary.
2.	White glabrous	× Ditto	Purple hoary.
3.	Cream glabrous	× White glabrous	Ditto.
4.	Any red or purple glabrous	× Any red or purple glabrous	Red or purple glabrous.

The truth of this account appears from the fact that in F_2 from cream glabrous × white glabrous all the coloured are hoary and all the whites are glabrous. Again, purple (hoary) *incana* × cream glabrous gives in F_2 all the hoary plants *coloured*, and all the glabrous plants *white*; while "white" (hoary) *incana* × sap coloured types gives in F_2 coloured hoary, coloured glabrous, and in addition tinging "whites" in both classes.

When a character is produced by the meeting of factors belonging to two distinct allelomorphic pairs, the F_2 ratio will be 9 : 7 (*i.e.* 3 + 3 + 1), and consequently, when in Sweet Peas and Stocks a coloured F_1 is produced from two non-sap coloured types, the F_2 ratio is 9 coloured : 7 white; but there are 4 gametically distinct types among the coloured and 5 among the whites. Most of these have been now recognised experimentally.

When F_1 is purple the coloured class consists of purples and reds. In both Sweet Peas and Stocks the ratio is 27 purple, 9 red, 28 white, composed thus:

$$27 : 9 : \underbrace{9 : 9 : 3 : 3 : 3 : 1}_{28}.$$

The purples are due to the presence of a "blue" factor B, allelomorphic to b, its absence. Unless C and R are both present, B cannot be perceived without breeding tests. The three pairs, C, c, R, r, B, b, by entering into all possible combinations according to the simple Mendelian system, give the results observed.

This scheme takes no account of the sub-classes which sometimes occur in both purples and reds. Several of these are merely superposed on the primary classes, while others are more complex and require further analysis. The distribution of the colours shows further complications when some coloured strains were introduced as original parents.

"Reversion" is thus seen to be a simple and orderly phenomenon, due to the meeting of factors belonging to distinct though complementary allelomorphic pairs, which at some moment in the phylogeny of the varieties have each lost their complement.

Pollen characters in Sweet Peas. Gametic coupling of a novel kind exists in this case. The whole generation in F_2 consists of 3 long : 1 round. The whites taken alone also are 3 long : 1 round. But in the purples there is a great deficiency of rounds, while in the reds they are greatly in excess. This result indicates that there is a partial coupling of the long pollen character with the factor B, and a corresponding coupling

of round pollen with b. This peculiarity only occurs in families which contain *both* purple and red members. The gametic output of F_1 in these cases is approximately

$$7AB + 1Ab + 1aB + 7ab,$$

where A is long, and a round pollen. This arrangement gives a close approach to the observed figures:

	Purple		Red		White	
	Long	Round	Long	Round	Long	Round
Observed	1528	106	117	381	1199	394
Calculated	1448·5	122·7	122·7	401·5	1220·5	407·4

THE PROGRESS OF GENETIC RESEARCH

An Inaugural Address to the Third Conference on Hybridisation and Plant-Breeding

[*Royal Horticultural Society Report*, 1906]

It is just seven years since, on the hottest day of a very hot summer, the first Conference devoted to Hybridisation and Plant-breeding assembled at Chiswick. Looking back on that occasion we realise what some of us even then suspected, that we were concerned in a remarkable enterprise. No such conference had taken place before, and our proceedings were of the nature of experiment. That definite results might come from that beginning we naturally hoped, but of those who endured the heat of that stifling marquee, or inspected the plants exhibited in that tropical vinery, not one, I suppose, anticipated that in less than a decade we should have such extraordinary progress to record. The predominant note of our deliberations in 1899 was mystery. In 1906 we speak less of mystery than of order.

When formerly we looked at a series of plants produced by hybridisation we perceived little but bewildering complexity. We knew well enough that behind that complexity order and system were concealed. Glimpses indeed of pervading order were from time to time obtained, but they were transient and uncertain. As casual prospectors we picked up occasional stray nuggets in the sand, but we had not located the reef, nor had we any machinery for working it if discovered.

Then came the revelation of Mendel's clue, with all the manifold advances in knowledge to which it has led. The most Protean assemblage of hybrid derivatives no longer menaces us as a hopeless enigma. We are sure that even the multitudinous shapes of the cucurbits, or the polychromatic hues of orchids—though they may range from one end of the spectrum to the other—would yield to our analysis. Methods for grappling even with these higher problems have been devised. The immediate difficulties are chiefly of extension and application. Thus the study of hybridisation and plant-breeding, from being a speculative pastime to be pursued without apparatus or technical equipment in the hope that something would turn up, has become a developed science, destined, as we believe, not merely to

add new regions to man's knowledge and power, but also to absorb and modify profoundly large tracts of the older sciences.

Like other new crafts, we have been compelled to adopt a terminology, which, if somewhat deterrent to the novice, is so necessary a tool to the craftsman that it must be endured. But though these attributes of scientific activity are in evidence, the science itself is still nameless, and we can only describe our pursuit by cumbrous and often misleading periphrasis. To meet this difficulty I suggest for the consideration of this Congress the term *Genetics*, which sufficiently indicates that our labours are devoted to the elucidation of the phenomena of heredity and variation: in other words, to the physiology of Descent, with implied bearing on the theoretical problems of the evolutionist and the systematist, and application to the practical problems of breeders, whether of animals or plants. After more or less undirected wanderings we have thus a definite aim in view.

The suggestive impulse to which this great progress is due came from without, but we take pleasure in the thought that the London Conference, and no less the second gathering at New York in 1902, did much to ensure the vigorous response which that long-awaited stimulus received. Of those who have taken a chief part in the advancement of Genetics several were with us then, and to the interchange of ideas which ensued may be ascribed much of the keenness and solidarity of purpose with which the Mendelian clue was followed out.

Conferences, like other stimulants, are, I believe, beneficial if not indulged in to excess. There are, however, special considerations which make it desirable that people with our particular interests should occasionally confer. Genetics constitute a subject of vast range. Each worker can have experience only of some small part. Nevertheless the various phenomena are so closely interrelated that the centre of progress may shift rapidly from one part of the field to another. No one, therefore, can safely neglect the advances made in his neighbour's territory. Sciences follow the plan of developing organisms in that they pass through stages of little differentiation, when parts are still doing the work of the whole. In these early stages inquiry must be comprehensive. The worker must be wary of narrowness. While he is engrossed and perhaps lost in the idiosyncrasies of orchids a discovery may be made in regard to peas, or it may even be mice or lepidoptera, which is just what the orchidist requires to clear away his own obstacles. Not even the time-honoured

distinction between things botanical and things zoological is valid in Genetics, and I notice with satisfaction that though we meet as guests of the Royal Horticultural Society, and though by the nature of the case plants figure most in the bill, yet animals are by no means excluded.

Now Conferences, especially those informal gatherings which are to make so pleasant a feature of our present programme, offer exceptionally good opportunities for the acquisition of knowledge of this comprehensive character. In the course of these meetings we shall gain information and suggestions that would not be attainable by months of search in the best ordered library.

There is another reason why the subject of Genetics is particularly appropriate to the deliberations of a Conference. I find this reason in the fact that practical and scientific workers here have equal need of each other's aid. I hesitate to add that they have equal prospects of benefiting from the partnership; for while it is clear that the mind of the practical breeder is stored with the experience that the physiologist requires, it is less certain that the practical man would recognise that the scientific experimenter had much of great value to impart to him yet. To this question of the practical evaluation of genetic discovery I will again refer, merely for the present noting the fact that two quite distinct classes of workers are interested in this one class of facts, and that such meetings give a capital opportunity for them to compare experiences and take stock of each other's progress. For the success of our meetings it is essential that neither the practical nor the more strictly scientific aspect should unduly prevail to the exclusion of the other. There is then abundant reason for our coming together, and it is not without due sense of the importance of the occasion that I have accepted the great honour of presiding over your deliberations.

In the few moments which I can now claim it is impossible to enumerate, and much more so to demonstrate, the genetic discoveries made by various workers, here and abroad, since last we met. Much of this information will be given in the papers communicated to the meeting. We have with us to-day several distinguished pioneers of these inquiries. We are looking forward to hearing them speak for themselves.

It seems to me, therefore, that I shall most fitly inaugurate these proceedings by attempting with the utmost brevity to state the position which genetic inquiry has now reached. The difference

between the present and the former standpoint is well illustrated by taking two of the common ideas current among breeders and considering how each has gained in precision. The ideas I shall speak of are those conveyed by the terms "pure-bred" and "reversion." We have at last a critical appreciation of the physiological meaning of the term "pure-bred" as applied to a plant or animal. In a general way every breeder is familiar with the notion that some animals and plants are pure while others are not. We have long been accustomed to distinguish the two conditions in various ways—estimating purity sometimes by truth to parental type, sometimes by the uniformity of the offspring. Neither of these tests, as we now know, is valid. An individual may be impure though not sensibly different from the accepted type of its breed; and though continued breeding from an impure individual will probably in the end reveal impurity, yet several generations may be produced in succession without any such indication appearing. For example, if in a rose-combed breed of fowls that had bred true for generations, a single-combed bird were to appear, we might formerly have supposed either that one of the parents was impure, or that a new variation had occurred. We now realise that the introduction of the single comb may have taken place in some generation indefinitely remote, and the appearance of that feature in a perceptible form is due simply to the fortuitous meeting of two germ cells bearing the recessive character.

An individual is *pure-bred* when the two cells, male and female, from which it develops, are *alike in composition*, containing identical elements or characters. No long line of like progenitors is needed to produce a pure-bred plant. A purple sweet pea may, as we now know, have been bred from white grandparents exclusively, and yet be pure to the purple character. Conversely, a white sweet pea may be a seedling produced by the self-fertilisation of a purple-flowered plant, and yet be pure-bred in respect of whiteness. It matters not how the parents are bred. They may be mongrels, as heterogeneous in composition as packs of cards; but if from the two packs *similar* cards happen to be dealt, the product of these two cards is pure. And as in the cards we may consider their attributes of colour, suit, and number as distinct, so in the living thing we know that the several features or physiological characteristics may be treated as distinct in the cell-divisions by which the germ cells are formed.

From this separability or distinctness of the characters it follows that an organism may be pure-bred in one respect and cross-bred in

another. I need not remind my present audience that this conception of the unity and distinctness of characters provides the solid foundation which makes the science of Genetics possible. Instead of regarding genetic purity as a vague and problematical state which might or might not be attainable by a long course of selection and fixation, we now know exactly what it is and how it is produced.

It is evident that this is a piece of knowledge which the practical breeder can turn to account. In future he will work with individuals of tested composition and avoid masses, thereby greatly simplifying the work of selection and fixation. It is no exaggeration to say that in this branch of industry the breeder can now perform in four years what formerly he could scarcely have effected in twelve.

Take similarly the idea of Reversion, which was formerly invoked to account for the unexpected or the unwelcome, much as our ancestors appealed to the powers of evil. Reversion, as usually met with, is one of two very definite but quite distinct things. Commonly these recurrences of characters the breeder supposed he had bred out are merely due to the reappearance of a recessive character. Like the single comb spoken of above, these recessives never get the chance of appearing until they are introduced into the organism simultaneously from both sides of its parentage. A proof that any given reversionary character is merely a recessive can be got at once by observing that the reverting individuals, on being fertilised with themselves or with their like, will breed true, and at least will not reproduce the types from which they were extracted.

But in addition to this very simple sort of reversion there is another of a more complex and much more instructive kind—that which is generally known as *reversion on crossing*. The most familiar illustrations have been seen in pigeons, fowls, sweet peas, and stocks. This reversion to an ancestral form, which may be indefinitely distant, can occur even when types of absolute purity are crossed together. Such reversionary forms, unlike those first considered, *never* breed true in the first generation—the F_1 generation, as we call it—but in the F_2 generation there must in all ordinary cases be a small but definite percentage of reversionary individuals which are then pure-bred and thenceforth able to breed true. As we now can prove, the reappearance of the ancient characteristic is caused by the meeting together of distinct elements, long parted. In some unknown way these two factors "let each other off." Both factors must be present together in order that the feature in question may be developed.

The most complex illustration yet known of the effects of interaction between factors is provided by the ten-week stocks investigated by Miss Saunders, where, as we now know, an independent factor must be present in the plant to produce hoariness in the leaves; but even if this factor is present, the leaves are still glabrous unless it is also associated with the two other factors which are concerned with the production of flower-colour. How much further such analysis can be carried it is impossible to surmise. We see, as yet, no reason for supposing that the rules of inheritance now perceived in the case of the simpler properties or structures of animals and plants, are not applicable also to the features we regard as higher.

There is also a special kind of reversion on crossing made famous by Darwin's experiments on pigeons. Here the reversionary type is often not perceptible in F_1—the first cross-bred generation—but appears first in F_2 when the F_1 birds are bred together. Such a phenomenon has been made the subject of experiment by Mr Staples-Browne, and, as his results clearly indicate, the reason why the reversionary character, viz. the black barring on a blue ground, does not appear in F_1 is that this feature is obscured by the dominant blackness introduced by one of the parents. When the factors which produced the blue meet in F_2 birds, which do *not* also contain black, the Blue Rock colouring is then evident.

Such a case as this last is only an apparent difficulty. Nevertheless I should warn you that there is a large class of alleged reversions, of a kind more economically important than these, arising in ways not yet properly understood. I allude to the appearance of reversionary "rogues" among seed crops, where circumstances preclude the idea that we have to deal with mere recessives, and make it *primâ facie* unlikely that crossing is the provocative cause. For example, in the case of peas, such reversionary and wild-looking "rogues" with *round* seeds have been shown me by my friend Mr Arthur Sutton amongst crops of highly bred wrinkled peas. They are regarded as indications of that general degradation or degeneration which it is supposed would permeate all highly bred stock if selection were suspended. Now, though it is certain that in practice if the crops were neglected these hardy and productive "rogues" would soon prevail and overwhelm the pure and more delicate strain, we are no longer content to regard their presence as inevitable. In order to cope with them we must find out exactly what they are. By the strict method of breeding from individuals under proper precautions we have now the means

of doing this, and not till such investigations have been made need it be regarded as the inevitable property of any high-class variety to produce "rogues." Though as to this special case I make no prophecy, modern observations strongly suggest the paradoxical conclusion that there is no such thing as general degradation or degeneration. These phenomena are due to specific causes, most commonly to nothing more obscure than insect-crossing, or to unsuspected mixture with an unrecognised variety. I mention these things simply to illustrate the fact that though the precise physiological nature of reversion may seem a matter remote from practical life, it is not remote at all, but closely bound up with very important industrial considerations.

I have said that reversion on crossing is due to the meeting of long parted factors. Conversely, variation is often due to the separation or elimination of factors. In other cases it is almost certainly, though perhaps not quite certainly, due to the addition of *new* factors. Genetic research has thus provided the first indication of the physiological process which results in the birth of a variation. The consequences of this knowledge to the systematist and to the science of evolution I will not now pursue. By following the clue which the discovery of unit-characters has provided, the long range of phenomena first grouped in an orderly fashion by Darwin in *Animals and Plants under Domestication* can at last be subjected to precise inquiry. The proximate significance of many of these mysteries is indeed already made out. Only those to whom that treatise has long been a kind of "De Occultis Naturæ Miraculis" are able to appreciate what the new knowledge means to biological science.

Now once more as to the practical importance of all this. The breeder has two main objects in view: he wants to *create* novelties and to *fix* them. In the second of these objects he can, as we have already seen, expect help from Genetics. As regards the creation of new forms I must not speak so confidently. Nevertheless, there is a valuable class of novelties which are really novel only in so far as they recombine pre-existing characters of known types. Such recombinations, say of hardiness with desirable qualities of colour or shape, or of size or free-flowering habit with brilliancy, or of colours such as red and cream-yellow, belonging to distinct physiological systems, may be of great value to the breeder. If in the majority of such cases no infallible prescription can yet be given to produce the desired result, Mendelian knowledge often indicates the course which

is most likely to succeed. I am not straining the truth when I say that the right course in numbers of instances is one which an operator guided by common-sense alone would have studiously avoided.

But, apart from any specific claim as to the immediate economic value of genetic research, let me again take more general ground, and without fear of contradiction I will insist on the truth that with a critical knowledge of the meaning of "pure-bred" and "reversion" a new era begins. To confusion and guesswork, knowledge and orderly experiment succeed.

The conclusions I have named and others like them have been arrived at by statistical observations of a somewhat arduous kind. An account of these technical proceedings scarcely falls within the scope of this address. I must, however, dwell for a moment on the fact that the processes of segregation which bring about the outward and visible facts of heredity are in essence *symmetrical* processes. It has long been known, ever since the beginning of microscopical research, that cell-division often appears to be a symmetrical process. We have now learnt that this visible symmetry is in the main a true representation of the qualitative symmetry by which the qualities or characters are distributed among the developing germ cells. No one can yet declare that plans of distribution following some higher order of complexity do not exist; but analysis of the simple cases will keep us employed for many a year, and not till the symmetrical phenomena of heredity have been exhaustively explored can we contemplate a further expedition into the unknown. Of one thing at least we may be sure: that heredity is a regular phenomenon, in many of its manifestations simple and amenable to experimental methods of research. To have said as much in 1899 would have been only to make a pious ejaculation of personal faith. Before our meeting in 1902 the change had begun. We could deal with simple cases involving only two types of individuals. When a family contained on an average three of one type to one of another, or equal numbers of both, we knew what the fact meant. Now we can deal with much more difficult cases. The number of types does not trouble us. We understand the ratios 9 : 7 and 9 : 3 : 4 and 27 : 9 : 28, with many variations on these simpler themes. All these can be shown to be produced by the chance combinations of germ cells or gametes produced by symmetrical divisions.

But ever in our thoughts the question rings, what *are* these units that bring all this to pass, which in their orderly distributions decide

so many and perhaps all of the attributes or faculties of each creature before it is launched into separate existence? Colour, shape, habit, power of resistance to disease, and many another property that might be named, have one by one been analysed and shown to be alike in the laws of their transmission, owing their excitation or extinction to the presence or absence of such units or factors. Upon them the success or failure of every living thing depends. How the pack is shuffled and dealt we begin to perceive; but what are they—the cards? Wild and inscrutable the question sounds, but genetic research may answer it yet. Substances which excite disease or confer resistance, which preserve health or produce deformity, have been extracted, and it may not be more difficult to determine the nature of those critical factors which excite hoariness or colour in a plant.

It is not only the breeder of animals or plants who is concerned to know the truth about heredity. The results of genetic research affect every branch of physiological or sociological inquiry. Too long has science been content to explore the specialised and outlying functions of the body and to neglect the primary, central, and all-controlling function of heredity, on which the rest depend. Such neglect manifestly arose from the curious delusion that the laws of breeding were untraceable. With the Mendelian renascence that dark age has ended.

As a hopeful sign it may be noticed that in the United States the Carnegie Institution has lately equipped a station for the experimental study of evolution. In England, where through Darwin's genius the study of evolution first became a reality, the country in which the art of breeding has for ages occupied a place unequalled in other lands, no such opportunities exist. The pursuit of these objects demands facilities of a special kind, such as neither technical colleges nor the laboratories of the Universities are able to supply. Sooner or later, perhaps, an effort will be made to provide equipment of this kind in England. Whenever such an institution as that I contemplate comes to be designed, let it not be tied down to the pursuit of directly economical results. When someone says to me, "But can't you breed a Derby winner, or do something useful?" the reproach does not break my heart. In parenthesis let me remark that though, in the attempt to discriminate among animals all good enough to win, science may be as much at fault as common-sense, yet it would not surprise me if science were to devise a way of breeding even race-horses which would not produce about a hundred wasters for one fit to win—and yet I understand that common-sense remains content

with that rather modest attainment after two centuries and a half of steady trying.

The great advances in the application of science have generally become possible through discoveries made in the search for pure knowledge. Mendel's incomparable achievement, with all that it imports both to science and to practice, was brought about by the resolute determination to get to the bottom of one particular problem in hybridisation, a problem, too, without any very obvious practical concern, and we may rest assured that in no other spirit can natural knowledge be more profitably pursued.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY

[*Reports to the Evolution Committee of the Royal Society*, III, 1906, pp. 2—11]

Introduction

GRANTS received from the Government Grant Fund, and from the British Association, have been applied in part to the cost of the experiments upon which we now report, and in part to other researches which will be described hereafter. These sums would have been insufficient to enable us to carry on the work, and the scope of the investigation must have been greatly reduced had it not been for the generosity of Mrs Herringham, who in 1904 placed a fund at our disposal for this purpose. We wish to record our deep sense of obligation to her for this assistance.

The results obtained since the last Report have at length provided expressions which include most of the phenomena witnessed in the case of Sweet Peas and Stocks. These various results can now be treated as parts of a consistent whole, and a great simplification of statement is thus made possible.

Flower-colour in Sweet Peas (Lathyrus) *and Stocks* (Matthiola)

The phenomena in these two plants are essentially similar in that (1) a purple F_1 results from a cross between certain white[1] varieties; (2) F_2 consists of purples, reds, and whites. In each case subordinate colour-classes are present among the purples and among the reds. These minor distinctions are for the present disregarded.

The facts show that the appearance of colour is due to the association, in one zygote, of two factors belonging to independent allelomorphic pairs. The presence of either factor alone is insufficient to cause colour in the zygote. One of the two factors was brought in by each original parent.

Speaking of the two factors as C and R, the corresponding allelomorphs are respectively c and r, the absence of those factors. When

[1] White here means non-sap-coloured. In the Sweet Peas the two parent forms were white with long pollen, and white with round pollen. In the Stocks, the corresponding parent types were white glabrous and cream glabrous. The cream-colour is due to the presence of yellowish plastids, a character recessive to colourless plastids. This feature is quite distinct from sap-colour, and, in that respect, creams are true whites.

all the combinations of two such allelomorphic pairs are represented in F_2, there will, among 16 individuals, be on an average 9 in which both factors are present, and 7 having only one or neither of them, as shown in the accompanying scheme (Fig. 1).

The 9 will be coloured, the 7 will be white. There will be 4 gametically distinct types among the coloured and 5 among the whites. Many of these extracted types have already been recognised experimentally.

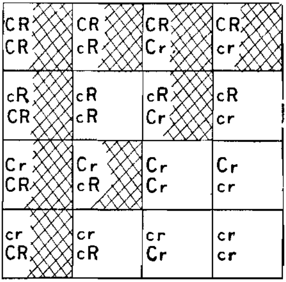


Fig. 1. Diagram showing the nature of the ratio 9 : 7 in F_2. The character, colour for example, appears only when C and R meet. Each square is a zygote, and the lettering shows its gametic composition. The hatched squares represent coloured plants; the plain are whites.

The ratio of coloured to white is thus 9 : 7. The coloured, however, consist of two main classes, purples and reds, in the ratio 3 purple : 1 red. The ratio of the three classes is therefore 27 purple : 9 red : 28 white. Such a distribution evidently results from the presence of a third allelomorphic pair, B, b, the presence or absence of a *blue* factor, which is dominant over the redness; but this only produces a perceptible effect when both C and R are also present. The relation of their distribution to the ordinary tri-hybrid scheme may be shown thus:

$$\underbrace{27 : 9}_{36} : \underbrace{9 : 9 : 3 : 3 : 3 : 1}_{28}$$

$$9 \qquad 7$$

In the Sweet Peas it is clearly the long-pollened white which introduced the factor B; for when crossed with red types it gave

purples, whereas the round white gave reds in such crosses. The occurrence on one occasion of red bicolor, the "half-reversion" of Report II, p. 84, in F_1 from long white × round white, was due to the circumstance that the particular long white used had no B factor (cf. scheme, p. 160).

In Stocks this factor was introduced by the *white* glabrous Stock, not by the cream glabrous; for F_1 from white × red is purple, but F_1 from cream × red is red (see p. 155).

Some outstanding problems are presented by the sub-classes of purples and of reds, which exist in both the Sweet Pea and the Stock F_2 families. Several of these differences depend on the presence of other simple allelomorphs, and are merely superposed on the primary classes, while others are of a more complex nature, which is not yet understood.

The fact is remarkable that in both Stocks and Sweet Peas certain lighter colours are dominant to the darker, in the sense that in families containing both, the darker can be bred from the lighter, while the contrary is impossible.

Thus in the Stocks light purple is to dark purple what in Sweet Peas the reversionary purple with blue wings is to the purple with purple wings; and light red or "flesh"-coloured are to the full red Stocks what the Painted Lady Sweet Pea with light wings is to the Miss Hunt form with magenta wings.

Certain cases in which a *coloured* type was used as an original parent gave results which cannot yet be brought into harmony with this scheme, but the majority now present no difficulty.

The results here summarised agree well with those obtained by Tschermak in *Phaseolus*, where a somewhat similar case of reversion in F_1 was studied. The chief difference lies in the fact that in our case the original parents were both white.

Mutatis mutandis, Correns' case in *Mirabilis* presents many points of similarity, but in that plant the pigmentary substances are evidently different.

The phenomena described (Report II, pp. 44 to 53) in *Salvia Horminum* are now obviously reducible to the same system, and the figures which we took to represent the ratio 2 : 1 : 1 are in reality[1]

[1] For instance, Experiments 15 and 17 (Report II, p. 50) give in F_2 respectively 59 purple, 25 pink, 34 white, and 255 purple, 92 pink, 114 white; together, 314, 117, 148, when the expectation is 324, 108, 144. Similarly, Experiment 13 gave F_2 26 purple, 17 white. At that time equality was the supposed expectation, and the excess of purples was remarked on. There can now be no doubt that the true ratio was 9 : 7 which would give 24·2 and 18·8.

examples of 9 : 3 : 4. It is likely that all plants possessing similar sap-coloured varieties will be found to conform to this scheme. We note, however, that in *Primula sinensis* (unpublished results of R. P. Gregory) blue has been shown to be recessive, and presumably, therefore, the nature of the pigmentary substances is different.

It is premature to discuss the physiological nature of the two factors which, when they meet, produce colour, but it is not inconceivable that they may yet be isolated.

Hoary Leaves in Stocks

The character hoariness in Stocks is similarly due to the simultaneous presence of two independent factors which we shall call H and K, allelomorphic to h and k, the absence of those factors. The F_2 results show that, generally speaking, hoariness, the result of the interaction of H and K, cannot be produced unless C and R, the colour-factors, are also present. The existence of *white*-flowered hoary strains creates a difficulty. As regards "white" *incana*, this difficulty is only apparent, for it is certain that "white" *incana* is in reality a coloured form. Its flowers tinge on fading, and its embryos have the deep green colour characteristic of purple-flowered types. The white hoary Bromptons, however, are a marked exception to the general rule. Their flowers are not in any way coloured, and their seeds have at most a slight green tinge (sometimes none). Bromptons have been little studied in these experiments, and as yet we have no clue to the nature of their peculiarity[1].

In a few cases (see *e.g.* Expt. 28 B) there are rather wide departures from the F_2 numbers indicated by this scheme, and it is no doubt just possible that these figures indicate some further complication. With these exceptions, there is now a satisfactory account of all the chief phenomena, many of which were previously quite paradoxical. For example, we had found that

1. Cream glabrous × white glabrous gave purple hoary
2. Cream glabrous × purple glabrous gave purple hoary
3. Cream glabrous × red glabrous gave red hoary
4. White glabrous × purple glabrous gave purple hoary
5. White glabrous × red glabrous gave purple hoary

but 6. Any red or purple glabrous × any red or purple glabrous gave red or purple *glabrous*.

[1] As white Bromptons × cream glabrous give red F_1, it is evident that they do not carry B.

These facts were not consistent with the simple supposition that cream, for instance, bore a factor α, which, when it met a factor β borne by, say red, gave hoariness. For since *white* × red also gives hoary F_1, the white must similarly bear α; but though on this reasoning white and cream are alike bearing α, yet when crossed they also give hoary F_1. The explanation is that the types have the following composition:

White glabrous	H and K	C or R
Cream ,,	H and K	R or C
Purple ,,	H or K	C and R
Red ,,	H or K	C and R.

Moreover, the whites and purples carry B, while the creams and the reds are without this factor.

That this is the true account appears from the distribution of characters in F_2. From cream glabrous × white glabrous, F_2 consists of coloured *which are all hoary*, and whites and creams *which are all glabrous*. When, however, cream or white glabrous is crossed with a sap-coloured glabrous, all the hoary are coloured in F_2; but of the glabrous some are coloured and some are white.

Again, F_2 from "white" *incana* × sap-coloured glabrous, contains *tinging whites* in both hoary and glabrous classes.

From these considerations it follows that hoary F_2 plants may be of three kinds—(1) those which give all hoary in F_3; (2) those that give 9 hoary to 7 glabrous; (3) those that give 3 hoary to 1 glabrous. All these kinds have been experimentally recognised (see R. p. 41)[1].

"Latency"; Resolution; Determining Factors

Cuénot showed that when in mice a new colour appears in F_1 from colour × albino, this is due to the introduction by the albino of a factor which, when it meets the colour brought in by the coloured parent, modifies it. For instance, when black × white gives grey (*i.e.* wild colour) F_1, this is due to a grey determining factor, brought in by the albino, meeting the colour brought in by the black. The grey determiner thus dominates over the black determiner to which the original black owes its blackness; and F_2 will be 9 grey, 3 black, 4 albino. Cuénot represents the allelomorphic pairs as—

Colour (C)	No colour (A)
Grey determiner (G)	Black determiner (B).

[1] [R. prefixed means pagination in original Report. Ed.]

More strictly, perhaps, we think they may be represented as

Colour	(C)	Absence of ditto (c)
Grey determiner	(G)	,, ,, (g)
Black ,,	(B)	,, ,, (b).

The arithmetical results are, of course, the same[1]. In the case just mentioned both parents can be regarded as homozygous in B, while the albino is also homozygous in G. But when grey × albino gives in F_2 3 grey : 1 albino, the fact that no new colour appears is due to the circumstance that the albino is homozygous in G. When the same cross gives in F_2 9 grey, 3 black, 4 white, the occurrence of the blacks proves that the albino carried no G, and that both the original parents were homozygous in B.

Albinos extracted from blacks cannot be bearing any determiner dominant to B; and if the blacks give no colours but blacks (and albinos), then the albinos so extracted must be homozygous in B, altbough they may still carry determiners recessive to B—that of chocolate, for example. If the allelomorphic pairs are expressed in the way indicated, the relation of the plant to the animal cases becomes clear.

Analysis of this kind is applicable to many and perhaps to all of the phenomena which we have hitherto attributed to resolution of a compound allelomorph, though as now appears they are merely expressions of a simple Mendelian process. The polymorphic F_2 of Sweet Peas and Stocks is now almost entirely reducible to terms of the same simple system.

Animal and plant cases differ remarkably in the fact that in animals colour has not yet been shown to be due to the meeting of two complementary factors. For no instance is known of two albino animals giving coloured F_1; and similarly the ratio 9 coloured : 7 albino has not been met with in any F_2 from coloured × albino in animals, though in plants such cases are not now very rare. Consequently, if in animals colour does depend for its appearance on two complementary factors (apart from *determining* factors, which exist in plants and animals alike), it must be recognised either that they have never separated, or, as is more probable, that one of them is present in all individuals, whether coloured or albino. Animals have probably reached the stage in which one only of the two factors may be absent, whereas in some plants both may be absent from the gamete.

[1] The correctness of this representation can be tested by crossing a wild grey mouse with a chocolate. If the view here expressed is right, *blacks* must appear in F_2.

A character such as colour, depending on double factors, or hoariness in Stocks, produced by four factors, may no doubt be properly spoken of as a compound character, and so we may speak of its "resolution," but in a sense different from that we originally intended. The compound is now seen not to be, in its entirety, a unit allelomorphic to another unit-character, but to be made up of several characters, each belonging to an independent allelomorphic pair. Consequently, in these cases, the conception of synthesis becomes superfluous; for the fact that a new type appearing in F_1 may breed true after F_2 is now shown to be an ordinary phenomenon of homozygosis.

Castle and others have spoken of the presence of a determiner, *e.g.* that for black, in the albino, as a "latency" of black in the albino. It should, however, be realised that it is not "black" as a whole which is latent. One of the factors needed to produce black is present —as a cryptomere, to use Tschermak's term—which cannot be made perceptible unless it meets colour in the zygote.

Reversion

The conception of reversion on crossing now takes a definite shape. Such reversion is simply the reappearance of a feature which had disappeared owing to the absence of one of the complementary factors. When two white Sweet Peas give a red bicolor F_1 there is reversion to the old "Painted Lady" type, because the two factors necessary for the development of that colour meet again. When the reversion is "total" (see Report II, p. 84, etc.) and F_1 is purple, the same two factors meet in the presence of the third element *B*, the determiner for purple. So for reversion in Stocks: when *C* meets *R*, the two whites give red F_1; if *B* is likewise present, a purple F_1. If both *H* and *K*, brought in by two glabrous types, meet in the presence of *C* and *R*, the further reversion to the hoary structure occurs. Somewhere in the history of the evolution of the modern types, the complementary elements have been split off and eliminated, giving rise to analytical variations.

Gametic Coupling

Early in the revival of breeding experiments, attention was called, especially by Correns, to the phenomenon of coupling between characters. Complete coupling has so far been most commonly met with among characters of similar physiological nature. Examples

of complete coupling between characters apparently quite distinct in nature are less frequent. As an illustration, we may refer to the apparently universal association of procumbent habit with dwarf stature in Cupid Sweet Peas, though in *Pisum* there is no such association between dwarfness and procumbency.

Examples of *partial* coupling have not hitherto been adequately studied. A remarkable case occurs in regard to the distribution of the pollen-characters in F_2 from the white long × white round Sweet Pea. There is here a partial coupling between the purple flower-colour and the long pollen. The whole mass of F_2 consists of 3 long : 1 round. The whites taken alone are also 3 long : 1 round. The *purples*, however, show a great preponderance of longs over rounds, about 12 to 1, while among the *reds* the rounds are in excess over the longs, being about 3 to 1. These peculiar distributions only occur in families which contain both red and purple members. Families (in F_3, for example) consisting of purples alone, or of reds alone, or of either associated with whites, have normal compositions. Evidently the abnormal distribution in some way depends on the mode of segregation of the factors B and b from each other. A close approach to the observed F_2 numbers would be given by a system in which each 16 gametes were composed thus:

$$7AB + 1aB + 1Ab + 7ab,$$

where A is long pollen and a round pollen,

	Purple		Red		White	
	Long	Round	Long	Round	Long	Round
Observed	1528	106	117	381	1199	394
Calculated	1448·5	122·7	122·7	401·5	1220·5	407·4

The distribution of the various characters may then be represented by the accompanying diagram (Fig. 2), p. 160.

The significance of such partial coupling is obscure, and it may result from several processes, between which no discrimination can yet be made. Nothing *à priori* limits us to the view that all characters are segregated at one division, but no system of symmetrical dichotomies will give the 7 : 1 system. If, however, the gametes AB and ab belonged to a generation later than aB and Ab, and were produced by three divisions after segregation had taken place, the numbers $8AB + 1aB + 1Ab + 8ab$ would result. Our statistics are not large enough to decide positively between 7 : 1 and 8 : 1, though the former

ratio fits best. There is no proof that all gametes of one flower are of the same order or generation counting from the fertilised egg, and, for example, we may feel sure that the male and female cells at least belong to different generations. Such a conception would introduce great complexity into these analyses, and in particular we should

CRB CRB	CRB CRb	CRb CRB	CRb CRb	CRB cRB	CRB cRb	CRb cRB	CRb cRb
CrB CRB	CrB CRb	Crb CRB	Crb CRb	CrB cRB	CrB cRb	Crb cRB	Crb cRb
CRB CrB	CRB Crb	CRb CrB	CRb Crb	CRB crB	CRB crb	CRb crB	CRb crb
CrB CrB	CrB Crb	Crb CrB	Crb Crb	CrB crB	CrB crb	Crb crB	Crb crb
cRB CRB	cRB CRb	cRb CRB	cRb CRb	cRB cRB	cRB cRb	cRb cRb	cRb cRB
crB CRB	crB CRb	crb CRB	crb CRb	crB cRB	crB cRb	crb cRB	crb cRb
cRB CrB	cRB Crb	cRb CrB	cRb Crb	cRB crB	cRB crb	cRb crB	cRb crb
crB CrB	crB Crb	crb CrB	crb Crb	crB crB	crB crb	crb crB	crb crb
63 : 1	57 : 7	57 : 7	15 : 49	63 : 1	57 : 7	57 : 7	15 : 49

Fig. 2. Scheme of distribution of colour-factors in F_2. From E. Henderson (Sweet Pea), white, long pollen × white, round.

The table is an expansion of that shown in Fig. 1, and exhibits the effect of the blue factor, *B*. The cross-hatched squares are purple-flowered plants; the single-hatched are red; the plain are whites.

The figures at the foot of each column show the ratio of long pollened to round pollened in each square of that column, on the hypothesis given in the text.

have to forego the natural view that segregation occurs at the reduction-division. There is another way in which the numbers 7 : 1 might be produced. If it were assumed that two other pairs of unknown factors *X*, *x*, *Y*, *y* were also present, and that the character

A is always coupled with either X, Y, or B, the result would be that the series of 16 gametes would consist of

$$7AB + 1aB + 1Ab + 7ab.$$

All the characters would then be distributed in one dichotomy, and the apparently partial operation of the coupling would be elucidated. The difficulty in the way of this suggestion is that no characters corresponding with X and Y have yet been identified which fulfil the required conditions.

This discussion cannot now be carried further. It is clear that gametic coupling, however caused, plays a large part in the phenomena of heredity. As another illustration of the coupling of a structural with a pigmentary character, we may mention that in some strains of Sweet Pea (to be described hereafter) the hooded standard is coupled with certain types of flower-colour; being, so far as we have seen, never found in purple—or red—bicolors. Presumably, the facts related in Report II, p. 91, indicate a similar partial coupling between the light axil and the peculiar contabescence of anthers.

Zygotic Coupling must be carefully distinguished from gametic. A character may be developed in those zygotes alone which possess some second character; but in the system of gametic distribution of the allelomorphs there may be no coupling between the two characters. For example, when the peculiar yellow flush is developed in the petals of a plant of *Primula sinensis* which bears the minute pollen of the long-styled type, the style does not rise above the anthers, constituting the "homostyle" condition[1]. Such plants are homozygous in respect of yellow flush and long-style pollen, but the two characters are entirely independent in their gametic distributions, as is proved by F_2 from homostyle × short style. Some very important illustrations of zygotic coupling are provided by the characters that are peculiar to one or other sex in sexually dimorphic species.

[1] W. Bateson and R. P. Gregory, *Roy. Soc. Proc.* LXXVI, 1905, p. 581. [This volume, p. 115.]

FACTS LIMITING THE THEORY OF HEREDITY[1]

[*Science*, N.S., xxvi, 1907]

MY first duty is to acknowledge the honour done me by the suggestion that I should deliver the address in this section. I need not say that I very highly appreciate the distinction thus conferred.

The fact that a heredity section has been constituted is surely a matter for congratulation. It is a sign that the study of zoology is passing into a maturer stage. For the past half-century zoologists have been chiefly occupied with the accumulation of morphological facts of structure and development. The perfection of microscopical methods had revealed regions in which knowledge could be readily advanced by simple means. We became, therefore, students of Cœlenterata, insects, Vertebrata, or whatever it might be, according as fancy or opportunity had specially attracted us to one or other of these groups.

Such work was interim work. It was making up arrears. This task is now practically accomplished. Almost all that can be seen by these simple means has been seen. One more phase is over. The division of our subject-matter according to the groups of the animal kingdom is no longer adequate.

We are trying for fresh points of attack. Our forces are disposing themselves in new formations, with fresh centres and a new front. In the organisation of the present congress the change has been recognised, and the creation of this section and of sections for experimental zoology and cytology testifies to the existence of new methods and new hopes.

Limitations of the animal classes do not trouble us. We take facts wherever we can find them. We are botanists to-day, zoologists to-morrow. The widening of interest which the study of heredity is bringing into modern zoology must prove a great benefit to the science.

When morphology was a new idea, everything was sacrificed to its pursuit. Physiology, systematics, all were discarded as useless lumber. Let us not repeat that short-sighted mistake. In the wider survey which we are attempting we shall need all these things. If we

[1] Address delivered at the International Zoological Congress, before the Section of Cytology and Heredity, August 23, 1907.

are to understand rightly the phenomena of specific difference—to take that problem only—we shall be glad of anything that the systematist can tell us, and of many deductions of pure physiology.

The study of heredity and variation—of genetics, to use our modern term—is itself a purely physiological inquiry, and as such it must range itself among other physiological inquiries; standing next beside, and looking constantly for support to, physiological chemistry.

The accidents of development which dissociated zoology from physiology were, as we are beginning to perceive, a misfortune, though perhaps an inevitable one. The botanists are happy in that their smaller dimensions have prevented such disruption. But let us hope that the dynamics of the zoological system may admit of the retention of that part of physiology which still adheres. Genetics will grow to be a big sphere one day; but may it never break off from the parent body whether as satellite or as sun.

Let us now examine the task which lies before us as students of genetics. Various descriptions of our objects may be made, referring to the phenomena of heredity and variation; their bearing on the theory of evolution, or on the origin and destinies of races. Stripped of all that is superfluous and of all that is special to particular cases, genetics stand out as the study of the process of cell-division. For if we had any real knowledge of the actual nature of the processes by which a cell divides, the rest would be largely application and extension. It is in cell-division that almost all the phenomena of heredity and variation are accomplished. Nothing is more easy than to witness this process. We may behold its minutest visible details when we please and as often as we please, and still no one has even a plausible guess as to the essential nature of the process. Two centres form: the parts collect round each. The two halves withdraw; or, if we may commit ourselves so far, repel each other, and there are then two cells instead of one. The likeness of those two cells we call heredity; their difference we call variation. If the two cells remain constituent parts of one body, we may speak of their likeness as symmetry or repetition; and their points of unlikeness we then call differentiation. But *how* the two centres were formed, not to speak of *why*, and how they came to separate, we have no surmise. Still less can we conjecture what it was that decided the distribution of differences between the two halves. No phenomenon of common life is so obscure.

By suitable means many of the finer details can be watched, but

the most meticulous observation has failed to disclose the essential truth which must yet be so near. I am speaking in a country where by the determination of vigorous observers a great school of cytologists has arisen who have greatly added to knowledge of the perceptible features. They will, I think, agree with me that were the powers of the microscope increased many times, it is unlikely that we should be very much wiser than we now are. Evidence of a different sort is needed.

Others by great ingenuity have tried to penetrate a little deeper by making models which in various ways can reproduce something of what is seen to occur, but the features thus represented are those which occur *after* the two centres are formed—the consequences, that is to say, of the division, not the division itself.

That remains a phenomenon unparalleled in the physical world, like consciousness, a distinctive property of living matter. By no confection of chemistry or mechanical contrivance can we yet fit together a system which will dichotomise and grow, dichotomise and grow, repeating the process again and again as long as certain materials are supplied to it.

The point on which I wish here to lay emphasis is the failure to conceive or to represent the dichotomy. Heredity, as we commonly see it, is much more than that, but the dichotomy is the one feature common to all its manifestations. I have sometimes thought that in our investigations of the later and more special phenomena of inheritance there is a danger of forgetting that this is the essential fact. In the visible rearrangement of the chromosomes, for example, in mitoses, occurrences so tangible and striking are witnessed that the observer can hardly avoid exclaiming, "This is the essential process of heredity," or "Those chromosomes which I can watch and count must be the physical basis of hereditary likeness." Attractive and stimulating as those wonders are to behold, the essential is still beyond. Heredity began in the explosion which impelled the chromosomes on their courses. If it were possible to identify the chromosomes ever so clearly as the physical bearers of hereditary characters, the problem of the division would remain, and I am strongly led to expect that it must be in some new light on the causation of the division that the way to attack the essential problem will be found. In this expectation I am glad to find myself in agreement with Dr Loeb, whose stimulating address we heard yesterday. The researches which he has so successfully inaugurated have brought the

problem of cell-division at last within the range of experiment; and if the nature of the explosion remains still inscrutable, Loeb's work has shown how the charge may be fired.

In our deliberations I anticipate that the more immediate question, whether the chromosomes are or are not the bearers of hereditary characters, will be fully debated. Without presuming to a definite opinion on this question, I venture to state what seem to me formidable difficulties in the way of this expectation. If the chromosomes were directly responsible as chief agents in the production of the physical characteristics, surely we should expect to find some degree of correspondence between the differences distinguishing the types, and the visible differences of number or shape distinguishing the chromosomes. So far as I can learn, no indication whatever of such a correspondence has ever been found. Besides this, although no very thorough investigation of the chromosomes of somatic structures has yet been made on an extensive scale, I believe that definite cytological distinctions between the nuclei of the various tissues *of the same body* have not been detected. If chromosomes were the chief governors of structure, surely we should find great differences between the chromosomes of the various epithelia, whicb differ greatly in their structure and properties. As these cytological differences have not been found consistently there, the prospect of successfully tracing them among the specific types does not look very hopeful.

Again, no correspondence between the chromosome numbers and complexity of structure has ever been asserted to exist. Low forms may have many; highly complex types may have few.

Then, on the contrary, very closely allied types may show great differences in these respects. As you are aware, Rosenberg has shown that one species of *Drosera* has 20, while another has 10[1]. Again, Miss Lutz has found a similar state of things in *Œnothera gigas*, which has 28, while *Œnothera lata* has 14. Obviously this doubling means something definite, but it is not suggestive of the determination of specific difference. In *Aphis* Miss Stevens, on the other hand, has shown how wide a diversity may be presented by the chromosomes of forms so alike as to have passed for one species. These differences prove both too little and too much. I cannot but believe that all this evidence points to the conclusion that we are about to find among the chromosomes one more illustration of the paradoxical

[1] Important evidence as to these chromosome numbers has been published by R. R. Gates, *Botanical Gazette*, February and July, 1907.

incidence of specific difference, not the fundamental phenomena on which that difference depends. Among coleopterists punctulation is sometimes a feature of great systematic importance. To dipterists neuration and chætotaxy sometimes give useful critical data. In certain orders of *Lepidoptera*, the *Hesperidæ*, for example, the structure of the gonapophyses sharply distinguishes the species where all outward tests fail. But proceeding farther with each of these criteria, we are sure to come upon other groups where for a long series of diverse types the critical feature, so important elsewhere, may show no differences, or, on the contrary, may show hardly any stability. I have digressed outside my province in these remarks. My excuse must be that I have a rare opportunity of speaking to a great school of cytologists, who must, sooner or later, become the colleagues of us breeders in the attack on genetic problems, and I cannot resist saying how the facts strike an observer who is highly interested, and I may truly say unprejudiced. I suspect, then, that the specificity of the chromosomes may conform in general to these other phenomena of specificity.

There remains the suggestive fact that all that has been witnessed regarding the behaviour of the chromosomes is in fair harmony with the expectations which our Mendelian experience would lead us to form respecting the hypothetical "bearers" of varietal differences. On the other hand, with one striking exception, nobody has been able to connect a cytological difference with a character-difference in any instance. The exception, of course, is the case of the accessory chromosome which Professor Wilson so admirably demonstrated to us yesterday. Of that I shall speak again hereafter.

But though, in regard to these profounder questions, our knowledge is so defective, the results of experimental breeding are beginning to limit the problem in very definite ways. We know first the fact deduced from Mendel's original experiments with peas, that the bodily characters may result from the transmission of distinct unit-factors. According to Mendel's own conception these factors existed in alternative or allelomorphic pairs, of such a nature that only one member of any one pair can be carried by a gamete. Now though we cannot quite prove this first account to be wrong, it is nevertheless possible to express all Mendelian phenomena in terms of a simpler system, according to which the allelomorphism may be represented as consisting essentially not in the presence of separate factors for the dominant and for the recessive characters, but in the *presence*

of something constituting the dominant character which is *absent* from the recessive gametes. So satisfactory, indeed, are the results of this mode of representation that the probabilities are greatly in favour of its truth. Indeed, when the inter-relations of a complicated series of varietal types have to be dealt with, the presence-and-absence system, as we may call it, applies so readily that its correctness is scarcely doubtful.

In simple cases, for instance, in that of the rat, we may regard the colour grey and black as due to the operations of grey and black determiners acting upon a distinct factor for colour. According to the scheme promulgated by Cuénot, the two determiners, grey and black, are regarded as allelomorphic to each other.

Such a system, however, fails when, as in the case of mice, a third colour-type (in addition to the albino), viz. chocolate, has to be expressed. If, on the contrary, each determiner is regarded as allelomorphic to its own absence, a workable system is provided, which can deal with almost all the observed facts. The grey—or technically, agouti—mouse, then, contains all the factors. The black is black because it is minus the determiner for agouti, and the chocolate is wanting in the determiners both for agouti and for black. The relations of all the colour-types to each other are thus clear except in so far as the relation of yellow to the other colours is not quite satisfactorily accounted for on either system.

It is at present beyond my purpose to examine the suggestions made to deal with that particular difficulty, but leaving this special question on one side, we can draw the clear deduction that each of these varieties owes its existence to the absence or removal of some factor from the gamete of the type.

Conversely in other cases we perceive with equal certainty that the variety is due to the addition of such a factor.

To deal with this series of interactions, the simple conception of dominant and recessive is inadequate. We now need a term to denote the relation between dominant factors belonging to distinct pairs of allelomorphs.

Till lately we spoke of the relations between the grey colour of the mouse to the black colour in terms of dominance. Those terms, strictly speaking, should only be applied to members of the same allelomorphic pair. We can perhaps best express the relation between the grey and the black by the use of the metaphor "higher and lower," and I therefore suggest the term *epistatic* as applicable to characters

which have to be, as it were, lifted off in order to permit the lower or *hypostatic* character to appear. The same method of representation is, of course, applicable to the series of factors for pattern and for intensity of colour.

The case of patterns is in a special way instructive. Symbolically we can represent pattern as due to determining factors, like those which cause the tint or the intensity of colour.

Though justifiable as a symbolic representation, it is evident that the "factor" for pattern may really be a quantitative difference in the amount of one of the elements, presumably the chromogen. We may imagine that the colour appears on special parts, just as colour takes on the prepared surface of a lithographer's stone, always remembering that though the distinction between, for example, self-pattern, the Dutch-pattern and the English-pattern rabbit may thus be quantitative, the quantitative stages are fairly well defined.

The point is of interest inasmuch as when we come to estimate the minimum number of transmitting elements, it is superfluous to postulate additional elements as instruments in effecting these alterations in pattern, seeing that the change may very readily be imagined as due to a series of quantitative subtractions from the qualitative elements. If then we can thus regard the distribution of colour as dependent on subtraction-stages of some one element, say the chromogen, we are naturally led to refer the various intensities to another similar but also definite series of subtraction-stages in which the subtraction is spread over the whole field, and so on for the other qualities.

Two fairly distinct classes of difference may thus be presumed to exist, those depending on the qualitative elements and those due to quantitative subtractions from them. The latter may be again subdivided.

It is scarcely necessary at this time to repeat that almost all the subtraction-stages fully studied are fairly definite, and their existence implies no suggestion of general failure of segregation. Interesting experiments have recently been made by Castle and McCurdy, exhibiting positive results of selection inside the limits of one of these stages, viz. the so-called hooded type in the rat. Nevertheless, the maximum result attributable to selection in such cases is a modification within the limits of one particular varietal type.

Such evidence provides no escape from the conclusion that each genetic variety comes into existence by a special addition to or subtraction from the genetic equipment.

Of all the results to which experimental work has led us, that which to me is the most astonishing is the fact that the same systems of transmission should be followed by characters which, by whatever test they are judged, must be supposed to be most diverse in physiological causation. Naturally when we are dealing with changes in colour, for instance, or in the reserve materials of a seed, we surmise that the critical factor is a certain ferment, or rather, the power to produce that certain ferment. It is perhaps not too wide a stretch of imagination to regard susceptibility to fungoid disease as caused by some similar body. The diversity of these ferments must anyhow be very great, and it seems very strange that all these multifarious potentialities should exhibit gametic allelomorphism. Let us take an illustration. Colour, as we can prove in regard to several plants, and in regard to the plumage of fowls, is due to the meeting of two complementary factors. One is presumably a ferment. Recent research strongly suggests that it is a tyrosinase. The other is referred to as a chromogen. But whatever they are, the two bodies, or rather the factors which produce them, must be of utterly different nature, and yet, genetically, the two potentialities are treated similarly. Each is allelomorphic to the absence of such a power.

How much more astounding is it, that when we pass to qualities such as length of stalk and shape of flower, or of a cock's comb, the quality of the hair in rabbit, we still find the same rules in strict and undeviating operation. Any scheme of heredity on a scale comprehensive enough to deserve the title of theory must deal with this surprising fact.

There is another extraordinary feature in the behaviour of allelomorphs which, though known clearly in a few cases only, must certainly play a great part in the fuller elucidation of heredity. This is *partial gametic coupling*.

Mr Punnett and I have for some time been engaged in studying this phenomenon in the sweet pea (*Lathyrus odoratus*) and we have recognised indications of the same thing elsewhere. The section will perhaps forgive me for taking a botanical illustration. I have no doubt it will not be long before cases in animals are found.

In the sweet pea, then, we know experimentally about 11 distinct allelomorphic pairs. The actual number is, of course, much greater, but 11 have been critically demonstrated.

Of these characters some are concerned with the production of colour, others with the determination of form. The composition of

the F_2 families shows that several of these allelomorphs are not distributed independently among the gametes, but that certain combinations of characters occur with greater frequency than others. The first of these couplings to be made out was that between the normal *or long* pollen shape and the factor which determines *blue* colour. In the absence of the long pollen factor, the pollen is round. In the absence of the factor for blue, the flower colour is red. The coupling here is such that the F_2 numbers instead of being 9 blue-long + 3 blue-round + 3 red-long + 1 red-round, are 177 : 15 : 15 : 49, or very nearly so.

This system would be produced by the following gametic series: 7 blue-long + 1 blue-round + 1 red-long + 7 red-round.

It is not possible to decide strictly whether the series is 7, 1, 1, 7, or 8, 1, 1, 8, and, of course, the dichotomies which produce the one or the other of these systems must be entirely different, but the total of the series is either 16 *or* 16 + 2.

Now the other two instances of partial coupling show that the association is there in groups of either 32 or 32 + 2. In the first case the blue factor and the pollen shape are again concerned, but their proper system of coupling is disturbed by the presence of another element, that which governs the shape of the flower.

The three pairs of characters are then:

Dominant	*Recessive*
1. Blue	No blue, viz. red
2. Pollen long	Pollen round
3. Standard upright, having a central notch	Standard hooded, without a central notch.

Now, experiment has shown two things. First, that in these families there is a total and complete coupling of *blue* and *hood*. In other words, all gametes destitute of the upright standard factor have the blue factor, while all gametes bearing the upright standard are destitute of the blue factor. Consequently, there are in such families three types of plants, distinguishable by the shape and colour of their flowers:

1. Blue—hooded standard.
2. Blue—erect standard.
3. Red—erect standard.

Classes 1 and 3 are homozygous, but 2, which in this curious

instance happens to be the wild type of sweet pea, is here always heterozygous, like the blue Andalusian fowl. Consequently we meet the paradoxical result that of the three types produced in such a family the original wild form is the one which does not breed true, but continues to throw off the other two types.

It is only by a stretch of language that we can speak of the blue factor as coupled with the hooded shape; for the hooded shape is recessive, and thus may be regarded as the shape due to the removal of the factor for upright standard. A more strict way of describing the facts would be to speak of erect standard and blue factor as gametically alternative to each other. It is thus possible that we may have eventually to extend the conception of allelomorphism to cases like this where two characters, both dominant, due, that is to say, to the presence of some factor, are alternative to each other in the constitution of the gametes.

To return now to the distribution of the pollen characters in these families: the F_2 numbers prove that the coupling between the blue factor and the long pollen character is altered and becomes far more complete. When the hood standard is segregating from the upright standard at the same time as the blue is segregating from the red (viz. non-blue), and the long pollen from the round pollen, the gametic series is no longer 7 blue; long + 1 blue; round + 1 red; long + 7 red; round, but is evidently 15 + 1 + 1 + 15, unless, as is still possible, the actual numbers are 16 + 1 + 1 + 16.

A second case of this peculiar distribution exists in regard to the two characters, sterility of anthers and absence of colours in the axil; there the association is 15 (or 16) fertile ♂; coloured axil + 1 fertile ♂; green axil + 1 sterile ♂; coloured axil + 15 (or 16) sterile ♂; green axil.

The F_2 numbers resulting from the recombinations of two pairs of allelomorphs distributed independently, and according to various simple systems of partial gametic coupling, may be tabulated as follows. In each pair one of the factors is taken to be dominant over the other.

	AB	*aB*	*Ab*	*ab*	Total
No coupling	9	3	3	1	16
3 . 1 . 1 . 3	41	7	7	9	64
7 . 1 . 1 . 7	177	15	15	49	256
15 . 1 . 1 . 15	737	31	31	225	1024

and so forth.

Curiously enough, we have as yet no certain case of the coupling in a series of 8, viz. 3 + 1 + 1 + 3, though we can scarcely doubt that the system exists. There are, however, clear indications that couplings of a still closer order exist, and we may reasonably expect them to fall into systems corresponding with the series of powers of 2. This evidence will, in all probability, be of great assistance in the attempt to close in on the question of the moment at which the segregation of characters is effected and must be taken into account in any discussion of the nature of the dichotomies themselves. It becomes very difficult to suppose in these cases of close though still incomplete coupling that all the segregations occur at the reduction-division—or indeed at any single division—and we await with some interest the result of cytological studies of the antecedent stages in maturation. The difficulty reaches its maximum when we attempt to conceive the process of character distribution among the egg cells of plants. The male cells in plants and animals are so numerous that their numbers supply sufficient scope for the formation even of very long series of couplings. The egg cells, on the contrary, are few, and very often definitely grouped in special organs which again are arranged on a definite geometrical plan relatively to the gross anatomy of the plant. Even if the various accessory cells of the plant ovary are reckoned as belonging to the gametic series, the number seems still insufficient to allow for the development of a coupling which demands a long series for its expression. Is there, then, any organised system of differentiation connecting the several ovaries into a common plan? In maize and peas, where indications of this system might be expected to be found if they existed, the evidence is entirely negative, and that is all which can be positively asserted.

Turning now to another aspect of the problem, we have to look for facts which may help us to limit our search for causes of variation. We may, as I have said, assume that a vast number of variations are due to the addition or removal of definite factors. We begin, therefore, to have some dim conception of the nature of this class of variations, and at all events to appreciate that they must occur as definite and specific events. As to the causation of these events, there is almost no light. A few months ago, I think it would have been scarcely an exaggeration to have said there was none. It is, however, impossible not to recognise that the striking experiments lately published by Tower may be a positive contribution to this part of the inquiry. We can scarcely imagine that changes in temperature or

in moisture are the great or chief efficient causes of natural variation; still the fact that in Tower's experiments such artificial changes in conditions appear to have effected a modification in the germ cells of the potato beetle (*Leptinotarsa decem-lineata*) and to have permanently deflected the offspring into a recessive line, must be allowed weight in future discussions of these phenomena. Many points in that fine piece of work still remain to be cleared up, but a very remarkable beginning has been thus made. It is, perhaps, scarcely necessary to add a warning that though the response to change of conditions may have been direct, it must not be hastily concluded that the response is adaptive. The appeal to direct responses so common in evolutionary discussions of thirty years ago, was made to account for the complex adaptations of organism to environment. It is the total want of any evidence supporting that appeal which has driven most of us to disbelieve in the reality of any such claims, and there is nothing in the new evidence, I think, which should shake the attitude of resolute agnosticism which we have thus been led to adopt.

Similar reflections apply to another very curious instance of genetic change induced by more violent means. MacDougal states that by injecting zinc sulphate into the ovary of *Raimannia* he caused the plant to produce seeds which became small and depauperated plants, destitute of the ciliation characteristic of the parent species. These, in their turn, transmitted the new character to their descendants.

The facts which I have referred to as helping to limit our view have been drawn from the behaviour of a considerable range of characters and, as I have said, there are strange elements of similarity common to all. Respecting two very important classes of characters we still remain in almost total ignorance. Some years ago in attempting a provisional survey of variations I distinguished a special group of phenomena as *meristic*, that is to say, belonging to those occurrences by which division and repetition are effected in animals and plants. Obvious as the meristic differences are, we know very little as to the system followed in their inheritance. Only one case is clear, I believe. Farabee has shown that the peculiar condition of the human digits in which the fingers and toes have only two phalanges each, behaves as a simple dominant. Dr Drinkwater has very kindly sent me lately a table which he will shortly publish, showing exactly the same thing in an English family. In his family, as in Farabee's, the affected members were of very short stature. I cannot at all readily conceive how any ferment or other transmissible substance can be supposed

to be responsible for such a variation as this. It is true that the attacks of gall-flies or of fungi may excite branching, or proliferating cell-division in plants, and we may have to suppose that a poison can have this effect. Perhaps we may also imagine that the fine division of the hair follicles in Angora rabbits or Merino sheep may be due to the want of some substance which in the normal type inhibits or checks this excessive subdivision, but if we are to bring the two-phalanged digits into line with the rest of these observations we shall have to make an extreme demand upon the specific powers of chemical substances.

Polydactylism has thus far failed to give clear indications. Sometimes the inheritance is Mendelian, while in other strains or individuals dominance is so irregular that the descent becomes untraceable. Such irregularities of dominance here, as elsewhere, may be referred with some probability to the disturbing influences of other undetected factors. It is much to be hoped that cases of difference in the ground-plan numbers of some radial type will be found amenable to experimental tests. Here the problem may be found in a somewhat simplified form on account of the elimination of serial differentiation.

One most interesting class of characters remains untouched. I refer to right- and left-handedness. I can form no surmise as to the laws which will govern the descent of these characters. From Mayer's observations on *Partula* we learn that parents of either twist may bear young of either twist. The numbers in the uteri were so small that the absolute numbers were insignificant, and it may be an accident that no mixture of types was found in any one uterus. Direction of twist is a fundamental meristic phenomenon, being, as Crampton and Conklin have proved, determined as early as the first cleavage plane; and great light on the problem of cell-division might perhaps be obtained if the inheritances of these differences could be determined. The only case we have studied, that of *Medicago*, in which the fruits are right- or left-spirals according to species, proved unworkable, perhaps on account of the minute size of the flower and the roughness of the manipulations.

I must now refer to the one positive case alluded to above, in which a chromosome difference has been proved to be associated with a somatic difference. McClung, studying the accessory chromosome first observed by Henking, was the first to insist on its importance. He showed that in certain insects half the sperms have it and half are without it. This fact led him to make the natural suggestion that the

structure might be concerned in the differentiation of sex. This suggestion has been shown by Wilson to be correct, but the accessory body proves to be the peculiarity of the sperms which are destined to form *females*, not of those which will form males, as had been previously supposed. It was with no ordinary feelings of pleasure that in the past week many of us in Woods Holl, and again the large audience assembled in this room, beheld the fine series of photographs which so amply demonstrate Wilson's far-reaching discovery.

The definiteness of the facts is evident beyond all question, and whether the accessory body is in these types the "cause" of femaleness or only associated with that cause, we have at last the long expected proof that sex is determined in the germ cells, so far as these specific cases are concerned. In those cases we may even go farther and declare that the female is homozygous in femaleness, while the male is heterozygous in sex. Such a result accords well, I think, with the general conclusions to which breeding experiments, on the whole, point. For though great disparities between the proportion of the sexes occur in certain matings, these disparities seem to be obliterated in succeeding generations. If the one sex were homozygous and the other heterozygous, such impermanence of the divergences is what we might naturally expect[1].

Of course, the association of sex-distinction with an accessory chromosome is admittedly a peculiarity of certain types, but science proceeds by the discovery of prerogative instances, of which surely this notable illustration will long be remembered.

While knowledge has of late progressed so rapidly in regard to many genetic phenomena, we still know next to nothing of the facts relating to the incidence of partial sterility among heterozygous forms. Guyer found that the abnormality of which the sterility of hybrid pigeons is the expression, begins in the reduction-division and is apparent as an entanglement of the chromosomes which fail to divide. In many cases sterility is partial; and for example, a proportion of good pollen grains occurs mixed with the aborted grains. Fuller examination of these cases would probably lead to interesting results.

In selecting facts which tend to limit our outlook on the phenomena

[1] In these remarks I have of course in view the case where the actual numbers of the two sexes show strange departures from equality. The phenomena recorded by Doncaster in *Abraxas grossulariata* and by Standfuss in *Aglia tau*, where the proportions of the sexes belonging to two varietal types followed peculiar but consistent systems, are evidently to be referred to the effects of coupling, as Doncaster has shown.

of heredity I have naturally chosen to speak rather of features which are positive and mutually consistent than of the many negative and thus far conflicting items of evidence which must perhaps one day be allowed their weight. The real value of these negative and frequent doubtful observations is as yet so uncertain that they must be regarded rather as hints to be followed in the pursuit of facts than as facts already ascertained.

Allelomorphism, as we are becoming more and more disposed to believe, consists in the separation of a positive something from the absence of that something: More correctly, perhaps, we should say that the thing which conveys a certain power segregates, leaving in that cell-division no representative of that power behind. This allelomorphism is the one fact of which we have the clearest proof. It may govern, as we have seen, features of the utmost diversity. What then is that allelomorphism? An essential phenomenon of cell-division, it is not: for in homozygous organisms the products of division are alike. Any theory of heredity must include and recognise both these two kinds of division in its purview. We seek vainly as yet for a scheme by which these two sorts of division may be represented.

I do not know that analogy is helpful in these cases, but in my own mind I sometimes remember in this connection that the somatic divisions themselves are also of two types. There are segmentations which, as in radial animals or bilateral animals, divide similar parts from each other, and there are also the serial divisions by which series of differentiated segments are produced. It seems to me just possible that the heterogeneity among the differentiated segments may have some point of real resemblance to the heterogeneity of allelomorphs. I suggest this comparison with only a faint hope that it may prove sound.

Lastly, any scheme of heredity must be able to recognise the possibility of gametic coupling between allelomorphs belonging to distinct pairs, and though few such couplings have yet been proved, we have good reason to believe that yet other systems of couplings of much higher complexity exist.

Dr Loeb encourages us to look to chemistry for the fulfilment of our hopes, and often, as in the case of the sweet peas, of which I have spoken, we come very near indeed to something like simple chemical phenomena. Of chemistry I know little, but I would ask those who are experts in chemistry whether it is in harmony with chemical conceptions that, in all the range of characters with which we, breeders,

have dealt, no phenomenon suggestive of valency between characters has been observed. Everywhere we meet the fact that on an average the number of germ cells in which our allelomorphs are present is the same as the number in which these allelomorphs are absent. Whatever the kind of characters concerned, equality of number is the rule. While, therefore, we see very readily that the operations of the allelomorphs are due to chemical action, allelomorphism itself can not be expected to prove a chemical phenomenon in any simple sense. Allelomorphism is rather to be compared to the separation of substances which will not mix, and it is not impossible then in some of our more complex cases we are concerned with various phenomena of imperfect mixture. The elucidation of this part of the subject must be left to the physicist.

I can not conclude without expressing something of the delight which I feel that biologists are at length devoting themselves in good earnest to genetic problems.

To those whose memories go back even to the International Congress of 1898 in Cambridge the change is indeed amazing. Then we spoke little of genetics—little, that is to say aloud, or in official programmes, though under our breath some of us were murmuring of these things. In this congress the voices that we dared not raise in 1898 are rather in danger of hoarseness from too much speaking. But, seriously, we students of genetics may look forward to the future with great confidence and hope. Those who next week will see Professor Davenport's magnificent institution at Cold Spring Harbour will appreciate that a wonderful and most hopeful beginning has been made. The work of Professor Davenport and his staff, of Professor Castle, at Harvard, of Professor Tower, at Chicago, and of others I might name, are all evidences that a great and combined advance has begun. We in Europe will bear our part also, and if we have not any very fine equipment we must console ourselves with the thought that light-armed troops may move the faster for a while. With their base on Cold Spring Harbour, on Woods Holl and the Biologische Versuchsanstalt in Vienna, the allied armies of genetics, cytology and experimental zoology start for the grand attack; and I think when we meet at the end of another period of ten years, there will be victories to record.

TROTTING AND PACING: DOMINANT AND RECESSIVE?

[*Science*, N.S., XXVI, 1907]

In his book, *The American Trotter*, Mr S. W. Parlin makes several allusions to the production of pacers by trotters which suggested to me the likelihood that the pacing gait may be a Mendelian recessive in the horse. In reply to my questions, Mr Parlin, who has kindly interested himself in the matter, assures me that he has never known a natural trotter produced by *two* natural pacers, though, of course, pacers are often produced by trotters. Mr John Thayer, of Lancaster, Mass., tells me that his experience agrees with that of Mr Parlin. Certain alleged cases to the contrary have proved to be given erroneously. It seems, therefore, that there is *primâ facie* reason to suppose that the trotting gait depends on some physiological factor which is absent from the pacer. My object in writing this letter is to suggest to American readers the desirability of investigating the subject more fully. The materials for doing so are not to be had in England. It is scarcely necessary to point out the extraordinary interest of this illustration of Mendelian inheritance, if it should prove to be genuine. No doubt either gait may to some extent be acquired artificially by training, but I understand that the distinction between the natural trotter and the natural pacer is so definite that doubtful cases are exceptional.

THE HEREDITY OF SEX

[*Science*, N.S., XXVII, 1908]

IN *Proceedings of the Zoological Society*, 1906, I, p. 125, Doncaster and Raynor described certain remarkable experiments respecting the inheritance of the moth *Abraxas grossulariata* and its variety *lacticolor*. This variety was originally known in the female form only. Experimental crossings showed the following results:

1. *Lact.* ♀ × *gross.* ♂ gave F_1 ♂s and ♀s all *gross.*

2. F_1 *gross.* ♀ × F_1 *gross.* ♂ gave *gross.* ♂s, *gross.* ♀s and *lact.* ♀s; no *lact.* ♂ being formed.

3. *Lact.* ♀ × F_1 *gross.* ♂ gave all four possible forms, *gross.* ♂s, *gross.* ♀s, *lact.* ♂s, *lact.* ♀s. The ♂ *lacticolor* thus raised were the first that had ever been seen.

4. F_1 *gross.* ♀ × *lact.* ♂ gave *all* ♂s *gross.* and *all* ♀s *lact.*

In discussing this curious series of facts Doncaster adopted Castle's view that each sex was heterozygous in sex, and that each gives off male-bearing and female-bearing gametes. He then shows that if it be assumed (1) that in the F_1 ♀ there is coupling such that the male ova all bear the *grossulariata* factor and the female ova all bear *lacticolor*; (2) that in the gametes of the male there is no coupling; (3) that in fertilisation union can only take place between gametes bearing opposite sexes; (4) that dominance attaches to the sex brought in by the ovum; the observed results would be produced.

On re-examination of the case we have found a much simpler and, as we think, more probable account of the phenomena. Two assumptions only are needed: (1) that the female is heterozygous for sex, femaleness being dominant, and the male a homozygous recessive; (2) that when in F_1 the two dominants, femaleness and the *grossulariata* factor co-exist, there is a repulsion between them, such that each gamete takes one or other of these two factors, not both. Such mutual repulsion of two dominants has already been shown to occur in the sweet pea when a plant is heterozygous for the upright standard and for the blue factor, constituting what must be regarded as a spurious allelomorphism between them[1].

The whole series of facts is then consistently represented as follows,

[1] *Science*, N.S., XXVI, p. 655. [This vol., p. 171.]

D and *R* representing the presence and absence of the *grossulariata* factor:

1. *lact.* ♀ × *gross.* ♂

RR ♀♂ | *DD* ♂♂

F_1 *gross.* ♂ *DR* ♂♂ — *gross.* ♀ *DR* ♀♂

2. F_1 *gross.* ♀ × F_1 *gross.* ♂

composition *DR* ♀♂ | *DR* ♂♂

gametes {*D* ♂, *R* ♀} | {*D* ♂, *R* ♂}

F_2 2 *gross.* ♂ *DR* ♂♂ *DD* ♂♂ — 1 *gross.* ♀ *DR* ♀♂ — 1 *lact.* ♀ *RR* ♀♂

3. *lact.* ♀ × F_1 *gross.* ♂

RR ♀♂ | *DR* ♂♂

1 *gross.* ♂ *DR* ♂♂ — 1 *gross.* ♀ *DR* ♀♂ — 1 *lact.* ♂ *RR* ♂♂ — 1 *lact.* ♀ *RR* ♀♂

4. F_1 *gross.* ♀ × *lact.* ♂

DR ♀♂ | *RR* ♂♂

gross. ♂ *DR* ♂♂ — *lact.* ♀ *RR* ♀♂

The numbers originally obtained were very wild and irregular, but on repeating the experiments Doncaster got results which are numerically very close to expectation[1].

Attention is drawn to this case as illustrating the great value of evidence respecting dissimilarity in reciprocal crosses for the elucidation of the problem of sex-heredity. We have long been engaged on a more complex case of this kind, the heredity of the black pigmentation of the Silky fowl, in its crosses with brown Leghorns and other fowls with light shanks. The facts there also point very clearly to a similar solution, but it may be some years before the evidence is complete.

On general grounds it seems to us probable that one and not both sexes of the same organism will be shown to be heterozygous for sex, and that the approximately equal output of the two sexes in ordinary

[1] *Nature*, LXXVI, 1907, p. 248.

cases is a consequence of this. Correns[1] has lately shown that his experiments with *Bryonia* suggest that in that plant it is the male which is heterozygous. Russo[2], from his experiments on rabbits, concludes that sex is determined by the ova, which he regards as male and female, respectively, or in Mendelian terminology, that it is the female which is heterozygous.

There is, we think, no reason *à priori* why in nature generally dominance should be the special property of one sex alone. We rather anticipate that dissimilarity will be found between the great groups in this respect.

Consistently with the view that in Vertebrata the female is heterozygous, the production of male secondary sexual characters ensues in the female consequent on ovarian disease, while castration of the male produces effects which may perhaps all be regarded as arrests of development. In the Crustacea, however, the work of Geoffrey Smith and of Potts on parasitic castration points to the converse conclusion, namely, that the male is there heterozygous for sex, assuming definite female characters when castrated, while in the female castration merely arrests development.

Correns refers to E. B. Wilson's facts respecting the accessory chromosome as supporting the view that the male is the heterozygous sex, and we have lately done the same[3]. Doncaster, however, has pointed out to us what must be a serious difficulty in the application of this argument; for if the male sex be dominant, it has then to be supposed that dominance attaches not to the presence of the accessory chromosome, but to its absence, since it is in the female that the accessory chromosome is paired. Great weight we think must be given to this criticism. Dominance, as we now suppose, is due to the *presence*

[1] *Bestimmung und Vererbung des Geschlechtes*, Borntraeger, 1907.

[2] *Atti Ac. Lincei*, 1907. Heape (*Proc. Roy. Soc.* B, LXXVI, 1905) described in the rabbit processes by which ovarian ova frequently degenerate, apparently as a normal occurrence. Mr Heape very kindly gave us an opportunity of examining his preparations, and it was impossible to avoid being impressed with the general resemblance which such degenerating ova bore to those which Russo regards as destined to become males. Consequently before that view of their nature is adopted, the relation of the so-called "male" ova to the degenerating ova will need very careful study; for it seems as yet not unlikely that those differences which Russo has taken to indicate maleness may prove to be due to incipient degeneration. Also as regards the important question of the alleged effect of lecithin in increasing the output of females, an opinion can scarcely be formed on the cases published by Russo, for these are declared to have been selected. It is to be hoped that the full statistics will soon be published.

[3] *Science*, XXVI, 1907, p. 658. [This vol., p. 175.]

of something which is *absent* from the recessive, and we are almost precluded from imagining that the absence of a chromosome can be a cause of the dominant quality.

In order to bring the facts of sex inheritance in the parthenogenetic forms (bee, aphis) into line with our view, it would perhaps have to be supposed that sex segregation in these types takes place not between gametes, but between the primitive soma and the germ plasm, so that the ova would all bear the recessive male character and the spermatozoa the dominant female factor. To discuss this suggestion in detail would, however, carry us beyond the scope of this note.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY

[*Reports to the Evolution Committee of the Royal Society*, IV, 1908, pp. 2–5]

THE present Report deals with the continuation of the experiments with Poultry, Sweet Peas, and Stocks.

Some account is given of our analysis of the various kinds of white plumage in fowls. We have been able to show that, in addition to the white which is dominant to colour, there are two entirely distinct whites which severally behave as recessive to colour, but on crossing give only coloured birds.

In our last Report we gave reasons for regarding the rose-comb as a comb on which an additional element, "roseness," had been superposed, and we suggested that the allelomorphic pair consists in the two states: presence of the factor for rose (R) and absence of that factor (r). The rose-comb is in reality a single comb modified by the presence of a "rose" factor. The omission of this factor enables the single comb to appear. The same considerations apply to the pea-comb, which is single + a pea factor. The true allelomorphic pair in each case is the *presence* of a given factor which is dominant to the *absence* of that factor. This view we have since been able to illustrate by another experiment (R. p. 18)[1], and recent experience inclines us to regard it as applicable to all Mendelian cases as yet investigated. As the acceptance of the "Presence and Absence" hypothesis seems to demand some general expression for such interrelation between factors belonging to distinct allelomorphic pairs, we propose the terms *epistatic* and *hypostatic*[2]. For example, the combless, the single-combed, and the rose-combed conditions may, in the light of our present knowledge, be regarded as forming a cumulative series, and we should speak of the factor for single as being dominant to the combless condition but hypostatic to the rose factor; and similarly the rose factor may be referred to as epistatic to the single.

Some experiments with Sweet Peas have led to an extension of our knowledge of the inheritance of stature in this species. A cross was made between the dwarf procumbent "Cupid" and a half-dwarf

[1] [R. prefixed denotes pagination in original Report.]

[2] Already suggested by one of us in *Science*, November 15, 1907. [This vol., p. 167.]

form known as the "Bush" Sweet Pea. The F_1 plants all "reverted" to the normal tall habit, and subsequent breeding from these demonstrated clearly that the case can be expressed as one of simple dihybridism (see R. p. 6).

The majority of our Sweet Pea work of the past two seasons was undertaken with a view to further elucidating the phenomenon we have termed gametic coupling. Experiments described in our last Report showed that the offspring of plants heterozygous for the blue factor and for long pollen can be classified (omitting the whites) as purples and reds in the ratio 3 : 1, and as plants with long and round pollen in the same ratio. But the distribution of the pollen among the coloured forms was complex. Instead of there being three long purples to each round one, there were actually about twelve; and the deficiency of rounds among the purples was compensated for among the reds, where they were three to four times as numerous as the longs. We pointed out that this peculiar distribution would be brought about if we supposed that the majority of purple-bearing gametes bore also the factor for long pollen, and that the corresponding majority of non-blue gametes were associated with roundness. We suggested that in the present case the choice lay between the following two gametic series from the F_1 plant:

(*a*) 8 purple long, 1 purple round, 1 red long, 8 red round.
(*b*) 7 ,, 1 ,, 1 ,, 7 ,,

The comparative merits of these two systems were discussed in Report III, and we are still unable to decide finally between them. The numbers, however, are somewhat more consistent with the scheme based on the 7 : 1 : 1 : 7 ratio.

During the past two years we have come across two cases among Sweet Peas in which the coupling is closer. One of these also relates to the factors for purple and pollen shape (R. p. 11), but the other has to do with two entirely different pairs of factors, viz. dark and light axil, and fertile as opposed to sterile anthers (R. p. 16). In both of these instances the distribution of characters in F_2 is in accordance with the view that the gametic series is on a 15 : 1 : 1 : 15 basis.

The undoubted existence of these two grades of gametic coupling in the Sweet Pea suggests that each may find its place in a scheme of increasing intensity of gametic coupling, such as is shown in the accompanying table, where the two allelomorphic pairs are represented by *Aa* and *Bb*:

Gametic series					Zygotes containing—				
AB	*Ab*	*aB*	*ab*		*A* and *B*	*A* only	*B* only	Neither *A* nor *B*	
1	: 1	: 1 :	1	= 4	9	: 3	: 3 :	1	= 16
3	: 1	: 1 :	3	= 8	41	: 7	: 7 :	9	= 64
7	: 1	: 1 :	7	= 16	177	: 15	: 15 :	49	= 256
15	: 1	: 1 :	15	= 32	737	: 31	: 31 :	225	= 1024
$n-1$	: 1	: 1 :	$n-1$	$= 2n$	$3n^2-(2n-1)$	: $2n-1$	: $2n-1$:	$n^2-(2n-1)$	$= 4n^2$

The first term in the series is a simple case of dihybridism in which no coupling exists. The second term we have not yet encountered. But we have an ample series of experimental data which satisfy the third term; and the experimental evidence for the existence of the fourth term rests upon two independent cases.

As we have indicated in the table above, there is a general expression for this series of terms. If the number of the gametic series be represented by $2n$, then the nnmber of zygotes formed by such a series is $4n^2$; and this number will be distributed in such a way that there will be $3n^2 - (2n - 1)$ zygotes with both dominants, two groups of $2n - 1$ with one dominant each, and $n^2 - (2n - 1)$ with neither dominant. It is obvious that, as the value of n increases, the terms containing n become relatively smaller in comparison with those containing n^2. The closer the gametic coupling the rarer become the two middle terms of the series which contain but one dominant apiece. And if n become very large, it is clear that the series

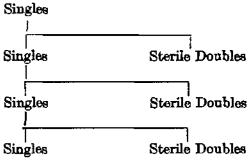
$$3n^2 - (2n - 1) : 2n - 1 : 2n - 1 : n^2 - (2n - 1)$$

will approximate to the series $3n^2 : 0 : 0 : n^2$. In other words, the greater the value of n, tbe closer we approach to a simple 3 : 1 ratio. *When aberrant forms occur in a series which is apparently of the usual* 3 : 1 type, it may be worth while examining them with a view to the possibility that they may represent the scarcer terms in a series resulting from close coupling.

During the past two seasons much of our time has been devoted to the inheritance of the hooded character in the Sweet Pea. The hooded standard behaves as a recessive to the erect standard, but in certain strains containing both red and purple flowers the hood is always associated with the latter colour (R. p. 9). In such cases we must suppose that all the "red" gametes bear the factor for the erect standard, and that this factor is absent from all the gametes which carry purple. We have, in Report III, referred to this phenomenon as one of gametic coupling, but strictly this expression is inapplicable.

In the cases of actual gametic coupling discussed in the last paragraph the association is always between the dominant or *present* factors of the different pairs; long pollen is coupled with purpleness, and the dark axil with the fertile anther. The "present" factors would seem to behave in gametogenesis as though they were attracted by one another. But here the phenomenon is of a different order. The two dominant factors, blueness and erect standard, seem to repel one another so that they are not both found in the same gamete; consequently only two kinds of gamete are produced instead of the four characteristic of a normal case of dihybridism, and the result is a simple 1 : 2 : 1 ratio such as we should obtain when dealing with a simple Mendelian pair. For this phenomenon we suggest the term *spurious allelomorphism*.

In Stocks, the work has been chiefly concerned with the inheritance of double flowers. The experiments have brought to light a phenomenon of a new order. Double Stocks being always totally sterile, both as regards male and female organs, are invariably the offspring of single-flowered plants. The succession in these double-throwing strains of singles is thus to be represented as follows:



Though always the offspring of singles, the doubles are nevertheless the majority, and the genetic mechanism by which this remarkable succession is accomplished remains problematical. The experiments have, however, contributed a first step towards the solution. *Singleness* is an ordinary Mendelian dominant to *doubleness* (Reports III, p. 44, and II, p. 29), but the singles in the double-throwing strains are of a curious composite nature. The double-throwing singles were crossed reciprocally with a strain of pure singles. The F_1 plants are all alike single; but an examination of F_2 from these plants revealed a remarkable difference between the results of the reciprocals.

For where the pure single was used as mother, F_2 from each F_1 contained doubles, whereas when pure single was the father, some of the F_2 families contained doubles and some were all singles. It follows

therefore that the pollen grains of the double-throwing strains must be all or nearly all[1] bearers of doubleness; but that the egg cells are of two kinds, those that bear singleness and those that bear doubleness.

The transmission of the cream-colour in the case of those single whites (known as "sulphur-whites") which throw double creams follows a similar system. The pollen grains of such plants are all or *nearly all*[1] *bearers of cream-colour, but the egg cells are of two kinds*, those which bear cream-colour and those which bear whiteness.

[1] Pending further inquiry, these statements must not be made in a universal form. Though hitherto no exception has been found in either case, it is still quite possible that a small proportion of the pollen cells in each case bear the dominant character.

THE INHERITANCE OF THE PECULIAR PIGMENTATION OF THE SILKY FOWL

[*Journal of Genetics*, I, 1911]

Introduction

During the past six years we have been engaged upon a series of experiments connected with the inheritance of the peculiar pigmentation of the Silky Fowl. A brief account of the general features of this interesting case has already been published by one of us[1], but as our experiments are now concluded we are able to give in greater detail the evidence upon which our views are based. As a description of the Silky Fowl may be found in any of the standard works on poultry it is unnecessary for us to dwell upon the characters of the breed except in so far as they enter into this particular series of experiments. One of its most remarkable features is the extraordinary abundance of black pigment which is generally distributed among most of the mesodermal tissues of the body. Seen through the thin epidermis this pigment gives the bird the appearance of a fowl with a black skin, deep purple comb and wattles, and dark slaty shanks. The iris is heavily pigmented, and the usually white earlobe takes on a more or less intense turquoise tint which is especially noticeable in the hens. The somatic peritoneum, the periosteum and pia mater are inky black from the pigment with which they are crowded. The splanchnopleure is much less pigmented, and the liver seen through this looks its normal colour. The muscles also have a blackish appearance, but we have not made any histological examination to determine the exact distribution of the pigment here. It is apparently confined to membranes of mesodermal origin, and is absent from the lungs, liver and other viscera, while at the same time the plumage is white. There is never any trace of it in the allantois, or other fœtal membranes.

Our experiments with this breed were begun with the idea of investigating the nature of the form of comb by which it is characterised, but we had not proceeded far before it became evident that the inheritance of the peculiar pigmentation promised more interesting and novel results. As the case presents features unlike any hitherto met with elsewhere it will be convenient if we give a brief outline of the

[1] W. Bateson, *Mendel's Principles of Heredity*, 1909, p. 181.

main results and of the interpretation before passing to a detailed examination of the experimental data.

General statement of results

The breed with which the Silky was originally crossed was a strain of Brown Leghorns which had been in our possession since 1899. The

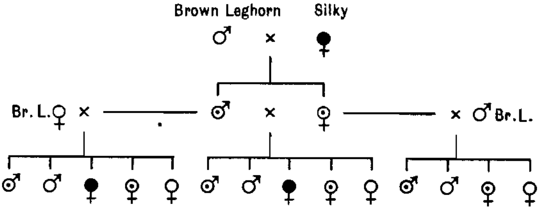


Fig. 1.

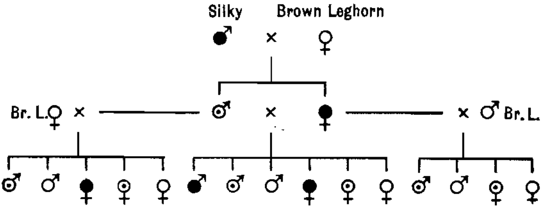


Fig. 2.

In these figures

represent unpigmented birds.

„ deeply pigmented birds.

„ birds with some grade of pigmentation other than the deeply pigmented type.

first indication of something unusual was the definite difference found in the reciprocal crosses between these two breeds. While the mating of Silky ♀ × Brown Leghorn ♂ resulted in chicks of both sexes with

little pigmentation, the mating of Brown Leghorn ♀ × Silky ♂ gave a markedly different result. From this mating the ♂ chicks had only a little pigment and were indistinguishable from those resulting from the previous cross, but the ♀ chicks were all deeply pigmented, differing but little in this respect from a pure Silky[1]. On breeding the F_1 birds together there resulted in either case an F_2 generation consisting of chicks of various grades of pigmentation ranging from the deepest pigment to none at all. The F_2 generation however presented certain distinctions according as a pigmented, or a non-pigmented F_1 hen was used (see p. 195).

The F_1 birds were also crossed with the pure Brown Leghorn and the results were strikingly different according as the sex of the F_1 was male or female. When the F_1 ♀ was crossed with the Brown Leghorn ♂ none of the offspring were deeply pigmented, and this was true for the pigmented F_1 ♀ as well as for the unpigmented. But when the F_1 ♂ was crossed with a Brown Leghorn ♀ about one in eight of the offspring were deeply pigmented *and these were always females.* To assist the reader in following this somewhat complicated case we append a rough scheme. It will be understood of course that the scheme gives no indication of the proportions in which the various classes are produced, neither for the moment do we attempt to differentiate between the various grades of pigmentation other than the fully pigmented state.

We may now state briefly the interpretation to which our various experiments have led us. We consider that three factors are involved of which two are directly concerned with the degree of pigmentation. These are (α) a *pigmentation* factor (P), and (β) an *inhibition* factor (I) which can prevent the full development of the pigmentation[2]. The various grades of pigmentation met with depend upon the various compositions of the zygotes in regard to these two factors; *e.g.* a bird of the constitution $PPii$ will be fully pigmented, a bird of the constitution $PpIi$ will be slightly pigmented, while birds of the constitution $ppII$, $ppIi$, or $ppii$ will be unpigmented (see also p. 202).

The third element with which we are concerned in these experi-

[1] The F_1 chicks all had coloured plumage and subsequent breeding showed that the white of the Silky behaved as a simple recessive (cf. *Rep. Evol. Comm. Roy. Soc.* IV, 1908). Our experiments have led us to infer that the pigmentation is quite independent of the colour of the plumage.

[2] The condition of the gamete from which either or both of these factors are absent we shall denote in the conventional way by the use of the corresponding small letters p and i.

ments is *sex*. Here we have made certain assumptions. We regard the female as differing from the male in possessing a special element, *F*, of which the hereditary behaviour is like that of any other Mendelian factor. Moreover, we consider that the female is always heterozygous for this factor, so that the zygotic constitution of a female is *Ff* while that of a male is *ff*. Further, we suppose that in such zygotes as are heterozygous for both *F* and *I* there occurs a

[**♂**] *iiPPff* gives gametes {*iPf*, *iPf*} × [♀] *IippFf* gives gametes {*Ipf*, *ipF*}

[♀] *IippFf* gives gametes {*Ipf*, *ipF*} × [♂] *IiPpff* gives gametes {*IPf*, *Ipf*, *iPf*, *ipf*} × *iiPpFf* [**♀**] gives gametes {*iPF*, *iPf*, *ipF*, *ipf*} × *IIppff* [♂] gives gametes {*Ipf*, *Ipf*}

Ipf *IPf* ♂	*ipF* *IPf* ♀
Ipf *Ipf* ♂	*ipF* *Ipf* ♀
Ipf *iPf* ♂	*ipF* *iPf* **♀**
Ipf *ipf* ♂	*ipF* *ipf* ♀

IPf *iPF* ♀	*IPf* *iPf* ♂	*IPf* *ipF* ♀	*IPf* *ipf* ♂
Ipf *iPF* ♀	*Ipf* *iPf* ♂	*Ipf* *ipF* ♀	*Ipf* *ipf* ♂
iPf *iPF* **♀**	*iPf* *iPf* **♂**	*iPf* *ipF* **♀**	*iPf* *ipf* **♂**
ipf *iPF* **♀**	*ipf* *iPf* **♂**	*ipf* *ipF* ♀	*ipf* *ipf* ♂

Ipf *iPF* ♀
Ipf *iPf* ♂
Ipf *ipF* ♀
Ipf *ipf* ♂

Fig. 3.

repulsion between these two in gametogenesis so that *F* and *I* do not pass into the same gamete. We may allude to the cases of the inheritance of the *lacticolor* variety of *Abraxas grossulariata*[1] and of the red eye of cinnamon canaries[2] in which similar phenomena can be shown to follow the same system of descent.

It must be expressly stated that the suggestion that females are

[1] Doncaster, L., *Reports to the Evolution Committee of the Royal Society*, IV, 1908.
[2] Durham, F. M., *Reports to the Evolution Committee of the Royal Society*, IV, 1908.

heterozygous for *femaleness* is offered without prejudice as to the possibility that males may also be heterozygous in *maleness*. The systems followed by the descent of colour-blindness[1] in Man and by that of the white eye recorded by Morgan in *Drosophila*[2] clearly point to the existence in those cases of a repulsion between a factor for maleness (M), and factors respectively for colour-blindness and for

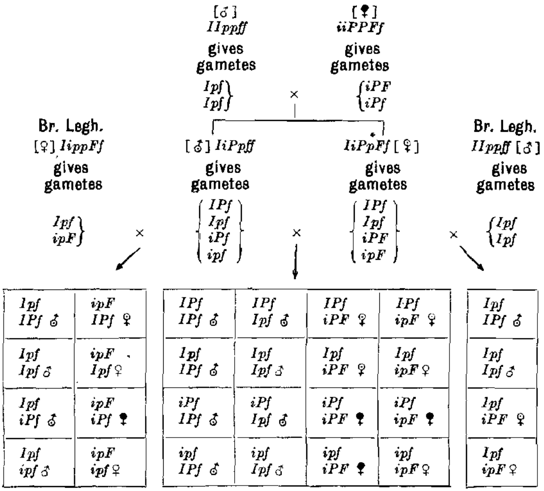


Fig. 4.

the red eye. The operation of the system of sex-limitation is similar in all these examples, the only difference being that in the one group the repulsion is from the factor F, in the other from the factor M.

Recognition of the existence of factors both for femaleness and for maleness of course involves the assumption that ova bearing F can only be effectively fertilised by sperms not bearing M, and *vice versâ*. For that supposition no independent evidence yet exists, and we note

[1] *Mendel's Principles*, 2nd imp., 1909, p. 195, note.
[2] Morgan, *Science*, N.S., xxxii, 1910, p. 120.

that Morgan[1] has made observations on *Cumingia* (Mollusca) distinctly unfavourable to it. At present however we think it is the most acceptable account of the facts ascertained both as to the heredity and the variability of sexual characters.

The Silky Fowl normally breeds true to the fully pigmented condition and we consequently represent the cocks and hens of this breed as *ffPPii* and *FfPPii* respectively. The Brown Leghorn on the other hand never produces pigmented birds and we therefore regard it as being entirely without the factor *P*. But it possesses the inhibitor factor *I*; and for reasons which will appear later the cock must be normally homozygous and the hen heterozygous for this factor. Constitutionally therefore we look upon the cocks and hens of this breed as being respectively *ffIIpp* and *FfIIpp*. To illustrate what we imagine to happen in the several generations produced by mating a Silky ♂ with a Brown Leghorn ♀ as well as in the reciprocal cross we have drawn up the appended schemes (Figs. 3 and 4) for comparison with Figs. 1 and 2. These schemes also indicate the composition on our hypothesis of the generations shown and we may now proceed to test their validity by the facts witnessed in these and other forms of mating.

DETAILED RESULTS OF THE VARIOUS CROSSES

1. The F_1 generation.

(a) From the Silky ♀.

[Nature of mating, *FfPPii* × *ffppII*]

We have bred from Silky ♀ × Brown Leghorn ♂ on two occasions and in neither case had any of the chicks more than a slight amount

TABLE I

Reference			Nature of mating	Males			Females		
				Full	Some	None	Full	Some	None
1905	Pen 16,	349	Silky ♀ × Br. L. ♂	—	5		—	2	
1907	„ 7,	495	„ „	—	8		—	8	
1909	„ 7,	150	F_2 ♀ × „	—	7		—	13	

of pigment (cf. Fig. 1). Many of these were reared and in the adult state were almost indistinguishable in general appearance from pure unpigmented birds. Careful examination however revealed traces of

[1] Morgan, Payne, and Browne, *Biol. Bull.* XVIII, 1910, p. 76.

pigment as patches either on the wattle, skin, or shanks. In most cases the presence of some pigment was most readily detected beneath the skin in the periosteum of the femoro-tibial or of the tarso-metatarsal joints. Dissection showed that some pigment was nearly always present in the ribs and in the occipital region of the skull. There was frequently a little peritoneal pigment, more especially in the region of the ribs, and some in the occipital pia mater. The amount of pigment varies somewhat and may be very slight. In some cases the chicks are recorded in our notes as being without pigment, but most of these records refer to birds which were not killed and critically examined. The extent to which the pigment development is inhibited exhibits individual variation, and it is likely that in some birds the inhibition is so complete that they are indistinguishable from birds which lack the pigmentation factor. Here we may mention also that we bred from a fully pigmented F_2 hen (♀ 150, see p. 199) with results similar to those which we obtained from the Silky hens.

(β) *From the Silky* ♂.

[Nature of mating, $FfppIi \times ffPPii$]

Our original Silky ♂ was mated at different times with two pure Brown Leghorn hens. The F_1 males from this mating were precisely similar to those produced from the reciprocal cross. The F_1 hens however were nearly as deeply pigmented as the Silky (cf. Figs. 2 and 4). To the one exception, a slightly pigmented ♀, we shall return later (p. 202).

TABLE II

Reference	Nature of mating	Males		Females		
		Full	Some None	Full	Some	None
1905 Pen 51, 404 1906 „ 18, 404	Br. L. ♀ × Silky ♂	—	8	8	—	—
1908 „ 18, 281 1909 „ 18, 281	„ „	—	29	31	1	—

2. The F_2 generation.

(α) *From the Silky* ♂.

[Nature of mating, $FfPpii \times ffPpIi$]

In Fig. 3 we have already indicated the results which are to be expected from this form of mating. One-quarter of the total offspring should be completely unpigmented while the remainder should be

equally divided between the fully pigmented and the partially pigmented classes, the expected ratio being three fully pigmented, three partially pigmented, and two unpigmented out of every eight birds. Moreover, the ratio should be the same for each sex. In Table III the results of seven such matings between F_1 birds are given. There is a slight excess of fully pigmented ♀♀ due to the unusually high proportion of such birds in one of the matings (1909, Pen 4, 329), but on the whole the facts are in close accord witb expectation.

TABLE III

Reference	Nature of mating	Males Full	Males Some	Males None	Females Full	Females Some	Females None
1907 Pen 15, 283	F_1 ♀ (full pig.) × F_1 ♂	11	6	4	9	11	9
„ 23, 114	„	2	6	1	6	3	3
1907 / 1908 „ 22, 121	„	6	7	6	6	6	4
1908 „ 5, 467	„	7	—	4	11	8	4
1909 „ 4, 329	„	11	13	9	22	8	6
„ 22, 148	„	3	3	3	5	2	1
1909 / 1910 „ 20, 374	„	11	20	7	15	17	11
	Total	51	55	34	74	55	38
	Expectation	*52·5*	*52·5*	*35*	*62·5*	*62·5*	*42*

(β) *From the Silky* ♀.

[Nature of mating, *FfPpIi* × *ffPpIi*]

As indicated in Fig. 4 expectation is here different from that in the preceding case where the F_1 ♀ was from the cross Brown Leghorn ♀ × Silky ♂. The slightly pigmented F_1 ♀ is here heterozygous for the

TABLE IV

Reference	Nature of mating	Males Full	Males Some	Males None	Females Full	Females Some	Females None
1906 Pen 9, 467	F_1 ♀ (unpig.) × F_1 ♂	1	3	1	2	—	2
1907 „ 11, 459	„	6	8	1	5	11	1
„ 20, 461	„	2	14	8	10	7	4
1908 „ 19, 459	„	—	2	3	2	3	—
„ 19, 393	„	3	14	8	5	7	6
„ 22, 467	„	—	1	—	4	—	—
	Total	12	42	21	28	28	13
	Expectation	*18·75*	*37·5*	*18·75*	*26*	*26*	*17*

inhibitor factor, I, and there comes into play the repulsion between I and F so that all the male gametes produced by such birds contain I, while this factor is carried by none of the female gametes. From this mating therefore we should not expect any fully pigmented males since every bird of this sex must contain I. Nevertheless, as the data in Table IV show, many of the males resulting from this mating were recorded as being heavily pigmented. By far the greater number of chicks in this generation were killed and recorded on hatching, and a peculiarity of the ♂♂ booked as fully pigmented lay in the fact that the toes of these birds were always light in colour. We regard these birds as of the constitution *ffPPII* or *ffPPIi* and suppose that in the presence of a double dose of the pigmentation factor the effects of the inhibitor are in considerable measure overcome in the younger stages. In corroboration of this view we may state that we reared several of these deeply pigmented ♂♂ and that they all became far less heavily pigmented in appearance as they approached maturity. In external appearance indeed they showed little more pigmentation than the F_1 cocks. This explanation is the natural one if we regard the constitution of the slightly pigmented F_1 ♀ as *FfPpIi*, and further evidence (p. 200) in favour of this view will be adduced from an entirely different set of experiments.

3. F_1 × **Brown Leghorn.**

(*a*) *Brown Leghorn* ♀ × F_1 ♂.

[Nature of mating, *FfppIi* × *ffPpIi*]

On our hypothesis this form of mating should give a specific result, for while the ♂♂ should all be either without, or with comparatively little, pigment, one-quarter of the ♀♀ should be fully pigmented (cf. Figs. 3 and 4). We have bred a considerable number of birds (nearly 700) in this way, and the figures given in Table V show that this expectation is closely realised. None of the 336 ♂♂ produced were deeply pigmented, while of the 362 ♀♀ 82 were deeply pigmented, a proportion approximating fairly closely to the expected quarter. We should add that owing to a deficiency of pure Brown Leghorns some of the hens used were light-shanked brown birds of Brown Leghorn extraction. With regard to the transmission of pigmentation these behaved similarly to the pure race.

TABLE V

Reference	Nature of mating	Males Full	Males Some None	Females Full	Females Some None
1906 Pen 9, 207	Brown ♀ × F_1 ♂	—	28	8	29
„ 33, 248	„	—	8	1	1
„ 33, 159	„	—	13	5	13
1907 „ 11, 203	„	—	34	8	24
„ 12, 264	„	—	13	3	8
„ 12, 159	„	—	19	3	18
„ 15, 347	Br. L. ♀ × F_1 ♂	—	34	11	37
„ 16.	2 Br. ♀♀ × F_1 ♂	—	18	2	14
„ 20, 129	„	—	22	7	19
„ 22, 101	„	—	42	8	28
„ 23, 98	„	—	24	7	18
1908 „ 5, 101	„	—	17	3	20
„ 16, 345	Br. L. ♀ × F_1 ♂	—	20	7	16
„ 22, 129	Brown ♀ × F_1 ♂	—	40	8	31
1909 „ 20, 347	Br. L. ♀ × F_1 ♂	—	4	1	4
	Total	—	336	82	280
	Expectation	—	*336*	*90·5*	*271·5*

(β) *F_1 ♀ (unpigmented) × Brown Leghorn ♂.*

[Nature of mating, *FfPpIi* × *ffppII*]

Two F_1 ♀♀ of this nature were crossed with a Brown Leghorn ♂ and gave 26 ♂♂ and 18 ♀♀ of which none were deeply pigmented. This again fits in with our hypothesis (cf. Fig. 4), for no deeply pigmented birds are to be looked for from this mating.

4. F_1 × Fully pigmented (*PPii*) birds.

(α) *F_1 ♂ × PPii ♀.*

[Nature of mating, *FfPPii* × *ffPpIi*]

The expected result from this form of mating is equal numbers, in both sexes, of chicks with deep pigmentation and of chicks with some pigmentation. We have made this mating twice with the following results:

TABLE VI

Reference	Nature of mating	Males Full	Males Some	Females Full	Females Some
1906 Pen 33, 349	Silky ♀ × F_1 ♂	5	2	3	5
1909 „ 17, 114	F_2 full pig. ♀ × F_1 ♂	20	18	19	22
	Total	25	20	22	27
	Expectation	*23·5*	*23·5*	*23·5*	*23·5*

These results are obviously in close accord with expectation, but it must be mentioned that ♀ 114 also gave one ♀ chick recorded as *without pigmentation*.

(*β*) F_1 ♀ (*slightly pigmented*) × *Silky* ♂.

[Nature of mating, ♀♂*PpIi* × ♂♂*PPii*]

Since on the hypothesis the gametes produced by the F_1 ♀ are ♀*Pi*, ♀*pi*, ♂*PI*, and ♂*pI* it follows that all the female chicks will contain *P* without *I*, while of the male chicks all will be heterozygous for *I* while half will be homozygous for *P*. In discussing the nature of the F_2 generation from this type of F_1 ♀ we have already seen reason for supposing that the male chicks of the constitution *PPIi* are practically fully pigmented on hatching, but that the pigment becomes much reduced with advancing age. Hence the expectation for the present type of mating is that all the ♀♀ will be deeply pigmented, and that the ♂♂ will hatch either as deeply pigmented chicks, or as chicks with some pigment only—these two classes being produced in equal numbers. Table VII gives the results of the two cases in which we have made this mating. While the general result is in accordance with expectation, the Table shows that there are two ♀♀ from each mating which are not fully pigmented. To these exceptions we shall recur later (p. 202).

TABLE VII

Reference	Nature of mating	Males			Females		
		Full	Some	None	Full	Some	None
1907, 1908 Pen 18, 459	F_1 ♀ (slight pig.) × Silky ♂	12	13	—	28	2	—
1907, 1908 " 9, 467; 1909 " 16, 467	"	12	18	—	28	2	—
	Total	24	31	—	56	4	—
	Expectation	*27·5*	*27·5*	—	*60*	—	—

(*γ*) F_1 ♀ (*fully pigmented*) × *Silky* ♂.

[Nature of mating, ♀♂*Ppii* × ♂♂*PPii*]

Since the gametes of neither parent carry the inhibitor factor and since those of one parent all contain the pigmentation factor, the expected result of this mating is fully pigmented chicks only, of both sexes. The mating has been made on three occasions and as Table VIII shows the results are in accordance with expectation.

TABLE VIII

Reference			Nature of mating	Males Full pigmentation	Females Full pigmentation
1907	Pen 18,	121	F_1 ♀ full pigmentation × Silky ♂	17	3
1907 / 1908	„ 18,	114	„ „	10	15
1907 / 1908	„ 9,	283	„ „	15	19

We have already alluded to the deeply pigmented hens which resulted from crossing the F_1 ♂ with the Brown Leghorn ♀. On our hypothesis these birds are in constitution *FfPpii* and consequently should give the same result as the deeply pigmented F_1 ♀ when crossed with a pure Silky ♂. We have made this cross on two occasions and in accordance with expectation all the chicks were deeply pigmented (cf. Table IX).

TABLE IX

Reference			Nature of mating	Males Full pigmentation	Females Full pigmentation
1907	Pen 18,	344	♀ *Ppii* × Silky ♂	11	12
1907	„ 9,	376	„ „	10	12

5. Crosses with deeply pigmented F_2 birds.

In the course of our experiments we have made crosses with two deeply pigmented F_2 birds, viz. ♂ 40 (from Pen 15, 283 of 1907) and ♀ 150 (from Pen 23, 114 of 1907). Each of these birds was as deeply pigmented in the adult stage as the pure Silky, and when bred together they gave only fully pigmented offspring (12 ♂♂ and 21 ♀♀). ♂ 40 was also mated with a pure Brown Leghorn ♀ and gave 21 ♂♂ with some pigment together with 33 deeply pigmented ♀♀. But he is recorded as giving also one deeply pigmented ♂ and 2 ♀♀ which were not deeply pigmented. To these exceptions we shall return and will merely state here that we regard them as due to a peculiarity in the behaviour of the Brown Leghorn hen. ♀ 150 behaved like a pure Silky when crossed with a Brown Leghorn ♂ (p. 193), and we look upon both these F_2 birds as of the constitution *PPii*.

6. The *ppii* strain.

In this account we have so far been concerned with the results of various crosses between the Silky and the Brown Leghorn breeds. By a happy accident we are able to adduce independent and cogent

evidence in favour of the interpretation which we have put forward. In 1907 we bought a Silky ♂ which proved to be heterozygous for P (*i.e.* $Ppii$). *Mated with an Egyptian hen, a brown bird with light* coloured shanks, he gave *unpigmented as well as deeply pigmented hens.* Two of these unpigmented birds were mated back to the heterozygous Silky ♂ in 1908 and as was expected gave deeply pigmented and unpigmented birds of both sexes, viz. 18 ♂♂ deeply pigmented, 15 ♂♂ unpigmented, 21 ♀♀ deeply pigmented, 17 ♀♀ unpigmented. In this way we were able to establish a strain of birds *containing neither the pigmentation nor the inhibiting factor in either sex.* These birds, on our system of notation, must be represented as $ppii$, and the possession of such a strain provided us with the means of testing the constitution of the F_1 (Silky × Brown Leghorn) birds in the simplest and most direct way.

The F_1 ♂ on the hypothesis produces four kinds of gametes in equal numbers, viz. fPI, fPi, fpI and fpi. Crossed with $Ffppii$ such a bird should give in both sexes equal numbers of birds with and without pigment. Again among the pigmented birds there should be equal numbers of deeply pigmented birds, and of birds with a small amount of pigment only. Table X shows that these expectations were closely realised in fact.

TABLE X

Reference			Nature of mating	Males Full	Males Some	Males None	Females Full	Females Some	Females None
1909	Pen 4,	408	♀ $ppii$ × F_1 ♂	1	3	1	—	3	4
	„ 17,	274	„	8	8	16	6	6	20
	„ 22,	261	„	5	4	5	3	3	8
			Total	*14*	*15*	*22*	*9*	*12*	*32*
			Expectation	*13*	*13*	*25*	*13*	*13*	*27*

We have also made a similar set of experiments to test the gametic output of the slightly pigmented F_1 ♀ (ex Silky ♀ × Br. L. ♂). The constitution of such birds on the hypothesis is $FfPpIi$ and owing to repulsion between F and I the gametes produced are of four kinds only, viz. FPi, Fpi, fPI, fpI (cf. p. 191). Mated with ♂♂ of the constitution $ppii$ such birds should give equal numbers of pigmented and unpigmented chicks in both sexes. And since the female gametes which contain P all lack the inhibiting factor, all the ♀♀ pigmented at all should be deeply pigmented. On the other hand all the male gametes of the F_1 ♀ which contain P contain also I, and consequently

none of the pigmented ♂♂ produced should be deeply pigmented. Table XI, which gives the details of four such experiments, shows how closely this expectation is realised, and offers strong corroborative

TABLE XI

Reference	Nature of mating	Males Full	Males Some	Males None	Females Full	Females Some	Females None
1909 Pen 3, 467	F_1 (slight pig.) ♀ × ♂ *ppii*	—	1	2	—	1	4
1909, 1910 ,, 13, 459	,,	—	11	9	16	2	12
1909, 1910 ,, 25, 393	,,	—	23	17	24	—	21
1910 ,, 22, 4 ♀♀	♀ *PpIi* × ♂ *ppii*	1	67	67	61	1	56
	Total	1	102	95	101	4	93
	Expectation	—	*99*	*99*	*99*	—	*99*

evidence of the view here taken of the nature of the gametes produced by this type of F_1 ♀. The five exceptions recorded we shall refer to again (p. 202).

THE CONSTITUTION OF THE BROWN LEGHORN HEN

While the Brown Leghorn ♂ is homozygous for the inhibiting factor, the ♀ is on our hypothesis always heterozygous for this factor. And since we assume repulsion to take place during gametogenesis between the factors *F* and *I* it follows that she produces two kinds of gamete, viz. *Fpi* and *fpI*. The possession of the *ppii* strain enabled us to devise a pretty experiment to test this view. By mating a Brown Leghorn ♀ with a cock of the constitution *ffppii* we obtained a number of unpigmented chickens of both sexes. On our hypothesis only the ♂♂ should receive the inhibiting factor, being in constitution *ffppIi*, while the ♀♀ should be *Ffppii*, and consequently lacking the inhibiting factor. This difference between the sexes with regard to the inhibiting factor should be brought out by a cross with fully pigmented homozygous birds (*PPii*), for while the females should give only fully pigmented chicks, the males may be expected to produce fully pigmented and partially pigmented chicks of both sexes in equal numbers. During the present year a cockerel (ex Br. Leg. ♀ × *ppii* ♂) was mated with a pure Silky hen, and four sister pullets were put with an F_2 fully pigmented ♂ (No. 40, ex Pen 15, 283 of 1907) already shown to be *PPii* in constitution. The results are shown in Table XII and are in accordance with expectation.

Table XII

Reference	Nature of mating	Males: Full	Males: Some	Males: None	Females: Full	Females: Some	Females: None
1910 Pen 8, 150	Silky ♀ × ♂ (ex Br. L. ♀ × *ppii* ♂)	1	4	—	3	3	—
„ 24, 4 ♀♀	♀♀ (ex Br. L. ♀ × *ppii* ♂) × ♂ *PPii*	18	—	—	26	—	—

Exceptions

In our account we have mentioned certain exceptions which occurred in several of the various matings. These are:

Table II, p. 194 .	ex Br. L. ♀ × Silky ♂	1 ♀ partially pigmented
p. 199 .	ex Br. L. ♀ × *PPii* ♂, F_2	2 ♀♀ partially pigmented 1 ♂ fully pigmented
Table VII, p. 198 .	ex F_1 (*PpIi*) ♀ × Silky ♂	4 ♀♀ partially pigmented
Table XI, p. 201 .	ex F_1 (*PpIi*) ♀ × *ppii* ♂	4 ♀♀ partially pigmented 1 ♂ fully pigmented

In all these cases the ♀♀ should have been fully pigmented and the ♂♂ should have been partially pigmented on our hypothesis. It will be noticed that wherever these exceptions occurred the mother was *a bird heterozygous for both F and I. These cases raise the question* whether the normal repulsion between *F* and *I* in such birds may not *occasionally break down, and whether in addition to Fi and fI* gametes they may not produce *FI* and the complementary *fi* gametes. This appears the more likely as in two out of the four cases a fully pigmented ♂ also appeared as an exception; and in Table VII even if such birds appeared they would not be noticed, since fully pigmented ♂♂ are one of the classes normally produced from the mating of slightly pigmented F_1 ♀ and the Silky ♂. We incline therefore to think that upon occasion the repulsion between factors may be imperfect, though whether this imperfection is sporadic, or whether it can be conceived as part of some orderly scheme we do not yet know enough to say.

The Grades of Pigmentation

The dependence of pigmentation upon the presence or absence of two factors (*P* and *I*), as well as upon the heterozygous or homozygous condition of the individual with regard to either or both of them, would naturally lead the observer to look for a considerable range of variation in the pigmented condition. For in the full zygotic series are the nine possible combinations, *PPii*, *Ppii*, *PPII*, *PPIi*, *PpII*, *PpIi*, *ppII*, *ppIi*, *ppii*. The great majority of the chicks with

which we dealt in these experiments were killed and recorded on hatching, and our practice was to refer them in so far as pigmentation was concerned to one of the following grades, viz. none, faint, slight, some, moderate, much, full, very full. Though not corresponding accurately to the various zygotic constitutions, these empirical grades nevertheless afford some indication of them. Where P is not present the bird is always unpigmented, though with regard to I it may be either II, Ii, or ii. Where I is absent the bird is nearly always fully pigmented whether homozygous or heterozygous for P, though it is probable that chicks recorded as with much pigment may sometimes have been in constitution $Ppii$. The birds classed as "very fully" pigmented were probably in most cases $PPii$ though sometimes they may have been exceptionally deeply pigmented birds of the constitution $Ppii$. Where both P and I are present some pigment would appear to be always present though the amount is subject to fluctuation. Thus F_1 birds of both sexes (ex Silky ♀ × Brown Leghorn ♂), and the ♂ birds (ex Brown Leghorn ♀ × Silky ♂) are of the constitution $PpIi$, but in respect of the intensity of their pigmentation they might belong to either of our three classes "slight," "some," or "moderate," and our experience has been that these classes grade very much into one another. Birds with "much" pigmentation are in general either $PPII$ or $PPIi$, though an occasional bird of the $PpIi$ class might be referred to this group. The class $PpII$ is doubtless to be found among the birds with "faint" or "slight" pigmentation.

The grade of pigmentation would also appear to differ somewhat in the two sexes, for among birds similarly constituted for these two factors P and I the females are generally a little more pigmented than the males[1].

This case of the Silky pigmentation is interesting in connection with the production of intermediate forms. In an F_2 family bred from Silky ♀ × Brown Leghorn ♂ all the nine possible zygotic combinations of P and I occur in one or other sex. It would be possible to choose birds of such breeding and to arrange them in a series exhibiting continuous gradation from full pigmentation to none at all. Yet we now know that such a series is due to the interaction of three definite factors (inclusive of the sex factor), and that the continuity in variation manifested is in reality founded upon a

[1] This fact is interesting in connection with the common experience of fanciers that in black-feathered breeds which have yellow skins, it is easy to obtain males with clear yellow shanks, but the females almost always have some black pigment in the shanks.

discontinuous basis. Moreover, we may point out that the mating of partially pigmented males of the constitution *PPIIff* with partially pigmented females of the constitution *PPIiFf* would result in the establishing of a race breeding true to an intermediate condition of pigmentation in spite of the underlying discontinuity involved.

Silky crosses other than with the Brown Leghorn

During the course of our experiments we have crossed the Silky with other fowls beside the Brown Leghorn, but as the crosses with the last named promised the most definite results our attention and resources were mainly devoted to these. We may however mention a few points of interest which have arisen in connection with some of the other crosses.

Our original Silky ♂ was mated in 1906 to a white Rosecomb bantam. All the chicks (5 ♂♂ and 7 ♀♀) were deeply pigmented on hatching though as they reached maturity the pigment became less marked in the cockerels. A few cases are already on record in which a Silky was crossed with another breed and all the resulting offspring of both sexes were deeply pigmented[1]. It is worthy of note that in such cases the breed with which the Silky was crossed possessed dark shanks. This was certainly so for the Spanish used by Tegetmeier and Darwin as well as for the Rosecombs used by ourselves; and we infer, though this is not explicitly stated, that it was also true for the frizzled fowls used by Davenport.

We may mention two cases from our experiments which are consistent with this view. When a Silky ♂ was mated with a dark-shanked mongrel ♀ (F_2 ex White × Brown Leghorn) 2 out of the 13 male chicks produced were fully pigmented. The remaining 11 male chicks exhibited a varying amount of pigment, while all the 11 female chicks showed the full pigmentation (1906, Pen 18, 150). In the other case an F_1 ♂, ex Silky ♀ × Brown Leghorn ♂, was also crossed with a dark-shanked mongrel Leghorn hen bred similarly to the last (1906, Pen 9, 604). Out of the 19 male chicks from this mating two were deeply pigmented, while with light-shanked hens the cock gave the usual result (cf. p. 197). We must suppose therefore that the factor or factors upon which shank pigmentation depends can influence the factors concerned with the development of the pigment found in the

[1] Cf. Tegetmeier, *The Poultry Book*, 1873, p. 268; Darwin, *Animals and Plants*, 2nd ed. 1899, p. 253; Davenport, *Inheritance in Poultry*, 1906, p. 60.

Silky fowl, but at present we do not know sufficient about the nature of these factors to make any more definite statement.

Though our experiments have led us to infer that the strain of Brown Leghorns with which we worked was homogeneous in respect of the factor modifying pigmentation we nevertheless have evidence suggesting that this is not necessarily the case for all light-shanked birds. An example may serve to illustrate our meaning. During 1908 and 1909 the fully pigmented F_2 ♂ mentioned on p. 199 was crossed with a Brown Leghorn ♀ and gave a typical result, viz. slightly pigmented ♂♂ and fully pigmented ♀♀. During both of these seasons he was also run with a light-shanked ♀ belonging to our recessive white strain[1]. With her he gave 19 male chicks varying from slight to moderate pigmentation, but of the 18 female chicks 8 were fully pigmented and 10 showed only a slight to moderate amount of pigment (1908–9, Pen 24, 53). From this and other similar experiments it seems natural to infer that some light-shanked hens may carry other factors capable of modifying the Silky pigmentation besides that which we have been able to demonstrate in the Brown Leghorn.

Lastly we may refer to a cross which we made between our original Silky cock and a hen which was homozygous for the dominant white factor (1907, Pen 18, 397). All the offspring (18 ♂♂ and 22 ♀♀) showed some pigment, sometimes a good deal, and this as a rule was distributed in small irregular patches, but we were unable to notice any difference between the two sexes. We think it not unlikely that the hen used was potentially a dark-shanked bird, and that the offspring of both sexes would have exhibited full pigmentation had not its development been in some way checked by the dominant white factor. The results however were complex and lack of opportunity prevented us from following up the cross, but we have thought it worth placing these cases on record since they indicate that radical differences in constitution may exist among light-shanked birds, and that the behaviour of our strain of Brown Leghorns with regard to the Silky pigmentation is not necessarily typical of birds with unpigmented shanks.

[1] An account of the origin of this strain will be found in *Reports to the Evolution Committee of the Royal Society*, III, p. 19, IV, p. 28.

ON GAMETIC SERIES INVOLVING REDUPLICATION OF CERTAIN TERMS

(With Plate I)

[*Journal of Genetics*, I, 1911][1]

IN a paper recently published[2] we gave a brief account of some peculiar phenomena relating to the coupling and repulsion of factors in the gametogenesis of the sweet pea and of several other plants. The view there stated was that if A and B represent two factors between which coupling or repulsion can exist then the nature of the F_2 generation depends upon whether A and B were carried into the F_1 heterozygote by the same gamete or by different gametes. If the heterozygote $AaBb$ is formed by the gametes AB and ab partial coupling between A and B occurs in F_2 according to a definite system, and it must be supposed that the gametes formed by the heterozygote belong to one or other of the series

$$3AB : Ab : aB : 3ab,$$
$$7AB : Ab : aB : 7ab,$$
$$15AB : Ab : aB : 15ab, \text{ etc.}$$

If on the other hand the heterozygote, $AaBb$, is formed by the gametes Ab and aB, repulsion occurs between A and B, so that only the two classes of gametes Ab and aB are formed. In the account to which we have alluded we supposed that such repulsion was complete, and that the two classes of gamete AB and ab were not formed. Our work on sweet peas during the present summer has led us to modify our conception of the nature of the gametes produced in cases where repulsion occurs, and this modification will perhaps be made clearer if we begin by giving an account of the experiments upon which it is based.

During the years 1906 and 1907 we were engaged upon an investigation of the inheritance of the hooded character in the sweet pea, of which an account appeared in Report IV to the Evolution Committee of the Royal Society, 1908, pp. 7–15. Among several thousand plants bred and recorded in this set of experiments there occurred a single individual (in Exp. 35, *R.E.C.* IV, p. 15) exhibiting striking peculiarities in the form of its flowers. These were small and much de-

[1] This paper also appeared in the 49th volume of the Brünn *Verhandlungen* which was published as a Mendel *Festschrift*.

[2] *Proc. Roy. Soc.* B, LXXXIV, 1911, p. 1. [This vol., p. 215.]

formed (cf. Pl. I, fig. 1). The standard failed to become elevated, the keel was cleft distally so that the anthers were partially protruded, while the stigma projected far beyond the petals, and was carried on in the line of the carpels instead of being abruptly bent at right angles to them as in the normal flower. At the time of its discovery in reference to the open "mouth," and the protruding "tongue" represented by the projecting style, the plant was dubbed "the cretin," by which term we shall subsequently refer to this peculiar malformation. The fact that the style protrudes is due to the malformation of the keel which is unable to curve the growing style and cause it to assume its natural position. Fuller experience of these cretins has shown us that the petals may sometimes be nearly as large as in normal flowers (cf. Pl. I, fig. 2), and that the standard may sometimes become elevated in the normal way (cf. Pl. I, fig. 3). The size of the flowers may vary considerably on the same plant, and hitherto where the larger form of flower has occurred the plant has also borne others more nearly resembling the original type. The degree to which the keel is cleft also shows some variation, but in all cases these cretins have the peculiar and characteristic straight stigma.

Our original cretin was found in 1907 and was used as the pollen parent to fertilise various sterile[1] sweet peas. The F_1 plants, which flowered in 1908, were all indistinguishable from normal sweet peas. The normal form of flower (N) was completely dominant to the cretin (n), and fertility (F) of the anthers was of course dominant to sterility (f). We may draw attention to the fact that the crosses were in all cases of the nature $Nf \times nF$, one of the two factors entering with each gamete. In the following year a single F_2 family was raised and consisted of 51 normal fertile, 30 normal sterile, 33 cretin fertile, and 1 cretin sterile[1]. The cretin character behaved as recessive to the normal flower, but the relative distribution of the different characters evidently pointed to some form of repulsion between the normal flower and fertility. Had it not been for the appearance of the single sterile cretin we could have regarded this case as one of complete repulsion between the factors N and F. The problem was to account for the sterile cretin, and at the time we were inclined to regard it as due to an unaccountable failure of repulsion between N and F. Lack

[1] In this family and in one of those grown later both light and dark axilled plants occurred. In each case the dark axil went in from the fertile cretin parent, and in F_2 there is some coupling between the dark axil and fertility. The numerical results however are complex and must be left over for discussion until more material is available.

of opportunity prevented us from following up this case in 1910, but in the present year we sowed the seed of the rest of the F_1 plants harvested in 1908 and obtained details of eight more families which are set out in the accompanying table (Table I).

TABLE I

Reference number	Normal fertile	Normal sterile	Cretin fertile	Cretin sterile
Number 5, 1909	51	30	33	1
„ 72, 1911	26	14	10	1
„ 73, „	21	12	12	1
„ 74, „	24	9	8	—
„ 75, „	22	4	4	2
„ 76, „	30	12	5	1
„ 77, „	78	43	32	3
„ 78, „	59	15	24	—
„ 79, „	25	12	15	2
Total	336	151	143	11
Expectation	*330*	*150*	*150*	*10*

These records show that the appearance of a small proportion of sterile cretins is a constant feature in these families and we suggest that their presence may be accounted for as follows. The repulsion between N and F is to be regarded as partial, and of such a nature that the series of gametes produced by the F_1 plant is NF, $3Nf$, $3nF$, nf. Such a series of ovules fertilised by a similar series of pollen grains would give rise to a generation consisting of 33 normal fertiles, 15 normal steriles, 15 cretin fertiles, and 1 cretin sterile. As the figures given in Table I show, this expectation is closely realised by the facts of experiment, and we have little hesitation in regarding this explanation as the correct one. Moreover, we are inclined to go further and to extend the principle to all cases of repulsion in plants. We consider then that where A and B are two factors between which repulsion occurs in the gametogenesis of the heterozygote formed by union of the gametes Ab and aB, the gametes produced by the heterozygote so derived form one or other term of the series

$$AB : 3Ab : 3aB : ab,$$
$$AB : 7Ab : 7aB : ab,$$
$$AB : 15Ab : 15aB : ab, \text{ etc.}$$

And if we take $2n$ as the number of gametes in the series we may generalise it under the expression $AB : (n - 1)\,Ab : (n - 1)\,aB : ab$. As the repulsion increases in intensity it is obvious that the zygotes

of the forms $AABB$ and $aabb$ will become relatively scarcer, for there will be only one of each of these two homozygous forms in the complete series of zygotes. At the same time the ratio of the three zygotic forms $AB : Ab : aB$ approaches more and more nearly to the ratio $2 : 1 : 1$ such as would occur if the repulsion were complete. This is brought out in the upper part of Table II where we have set out some of the gametic series in which partial repulsion is involved together with the series of resulting zygotes. The latter, as the Table shows, are covered by the general formula

$$(2n^2 + 1)\,AB : (n^2 - 1)\,Ab : (n^2 - 1)\,aB : ab$$[1].

TABLE II

	Gametic series				Number of gametes in series	Number of zygotes formed	Nature of zygotic series			
	AB	Ab	aB	ab			AB	Ab	aB	ab
ial repulsion om zygote of form $Ab \times aB$	1	$(n-1)$	$(n-1)$	1	$2n$	$4n^2$	$2n^2+1$	n^2-1	n^2-1	1
	1	31	31	1	64	4096	2049	1023	1023	1
	1	15	15	1	32	1024	513	255	255	1
	1	7	7	1	16	256	129	63	63	1
	1	3	3	1	8	64	33	15	15	1
	1	1	1	1	4	16	9	3	3	1
ial coupling m zygote of form $4B \times ab$	3	1	1	3	8	64	41	7	7	9
	7	1	1	7	16	258	177	15	15	49
	15	1	1	15	32	1024	737	31	31	225
	31	1	1	31	64	4096	3009	63	63	961
	63	1	1	63	128	16384	12161	127	127	3969
	$(n-1)$	1	1	$(n-1)$	$2n$	$4n^2$	$3n^2-(2n-1)$	$2n-1$	$2n-1$	$n^2-(2n-1$

Hitherto the only repulsion series which we have been able to identify with certainty is the one with which we have just dealt, *i.e.* $1 : 3 : 3 : 1$ series for the factors N and F.

It is probable, however, that the case of blue and long pollen[2] is one in which the repulsion is of the $1 : 7$ order. Up to the present time we have had four families of the mating $Bl \times bL$ and the 419 plants recorded in F_2 were distributed in the four possible zygotic classes as follows:

Reference number	Blue long	Blue round	Red long	Red round
Number 61, 1910	85	33	41	1
,, F 28, ,,	60	20	23	—
,, F 31, ,,	9	7	5	—
,, F 32, ,,	72	35	28	—
Total	226	95	97	1

[1] The general formulæ made use of here and in Table II are purely empirical, and offer a convenient way of calculating the nature of the zygotic series from any series of gametes.

[2] Blue in the flower colour (B) is dominant to red (b), and long pollen (L) is dominant to round pollen (l).

Though the evidence for partial repulsion rests here upon the single red round plant which occurred in family 61, it is in reality very much stronger than it appears at first sight, for the following reason. All the plants in the above four families were hooded, *i.e.* lacking in the factor for erect standard (E). As we have already pointed out[1], the three factors E, B, and L constitute a series such that if any two are brought into a zygote by different gametes repulsion occurs between them. Until the present round hooded red plant appeared we had never encountered this combination in any of our experiments. It cannot therefore be regarded as due to a stray seed from another family. And it is evident that if the repulsion between any pair of these three factors were complete such a plant could never arise. For in the normal course the *ebl* gamete could never be formed. Only two possibilities therefore are open. Either we must look upon it as an unaccountable mutation, or we must consider that the repulsion between B and L is partial. In the light of the evidence afforded by the cretin sweet pea we prefer the latter hypothesis, and we are inclined to regard the partial repulsion between B and L as of the 1 : 7 : 7 : 1 type. On this hypothesis we should expect one red round in every 256 plants (cf. Table II) whereas experiment gave 1 in 419. At the same time we recognise that the data are not yet suffieient to preclude the 1 : 15 : 15 : 1 system. It is worthy of note that the coupling between B and L is usually on the 7 : 1 : 1 : 7 system, and it would be interesting if in such cases as these the repulsion and coupling systems for a given pair of factors were shown to be of the same intensity. In most cases this could not be tested in practice owing to the very large number of plants required. Thus the coupling between erect standard and blue is on the 127 : 1 : 1 : 127 system, and if the repulsion were of similar intensity we should expect only one hooded red in every 65,536 plants. We may, however, state that in this particular case we have grown over 4000 plants without meeting with a hooded red, so that the facts, so far as they go, point to a high intensity of repulsion for factors exhibiting a high intensity of coupling. It is obvious that the relation can only be worked out where the intensity of repulsion is low, and it is hoped that the case of the cretin may eventually throw light upon this point when the system in which N and F are coupled shall have been determined.

The question now arises how these gametic systems are formed. In each the characteristic phenomenon is that the heterozygote produces

[1] *Proc. Roy. Soc.* 1911, p. 7. [This vol., p. 220.]

a comparatively large number of gametes representing the parental combinations of factors and comparatively few representing the other combinations. In describing the original case of coupling, namely that between the blue colour and long pollen in the sweet pea, we pointed out that no simple system of dichotomies could bring about these numbers, and also that it was scarcely possible that such a series could be constituted in the process of gametogenesis of a plant, in whatever manner the divisions took place. In saying this, regard was of course had especially to the female side, and this deduction has become even more clear in view of the fact that we now know a series consisting of 256 terms. It is practically certain that the ovules derived from one flower of the sweet pea, even if all collateral cells be included, cannot possibly be arranged in groups of this magnitude. A pod rarely contains more than nine or ten good seeds at the most, so that if we even reckon twelve potential seeds to the pod and eight potential gametic cells to the ovule, the total is still only 96, which is much too few[1]. Nevertheless our series of numbers is plainly a consequence of some geometrically ordered series of divisions.

There is evidence also from other sources that segregation may occur earlier than gametogenesis. Miss Saunders' observations on *Matthiola*[2] and on *Petunia*[3] proved that in those plants the factors for singleness are not similarly distributed to the male and female cells. The recent work of de Vries[4] on *Œnothera biennis* and *muricata* has provided other instances of dissimilarity between the factors borne by the male and female organs of the same flower. In all these examples it is almost certain that segregation cannot take place later than the formation of the rudiments of the carpels and of the stamens respectively. The only visible alternative is that in each sex the missing allelomorphs are represented by somatic parts of the sexual apparatus, which for various reasons seems improbable. There is therefore much reason for thinking that segregation can occur before gametogenesis begins, but there is no indication as to which are the critical divisions.

Now that we may regard the formation of four cells of composition

[1] From the fact that in maize the endosperm characters are the same as those of the seed itself we know moreover that segregation must have been completed before the divisions at which the male and female cells which constitute the endosperm are set apart.

[2] *Roy. Soc. Evol. Com. Rep.* IV, 1908, p. 36.

[3] *Journ. Gen.* I, 1911.

[4] *Biol. Centralbl.* XXXI, 1911, p. 97.

AB, *Ab*, *aB*, *ab*, as the foundation both of the coupling- and of the repulsion-series the problem is manifestly somewhat simplified. The time, excluding gametogenesis, at which we can most readily imagine four such definite quadrants to be formed is during the delimitation of the embryonic tissues. It is then that the plant is most clearly a single geometrical system. Moreover the excess of gametes of parental composition characterising the coupling- and repulsion-series must certainly mean that the position of the planes of division by which the four quadrants are constituted is determined with regard to the gametes taking part in fertilisation. Though the relative positions of the constituents of the cells may perhaps be maintained throughout the history of the tissues, it is easier to suppose that the original planes of embryonic division are determined according to those positions than that their influence can operate after complex somatic differentiation has been brought about.

At some early stage in the embryonic development or perhaps in later apical divisions we can suppose that the $n - 1$ cells of the parental constitution are formed by successive periclinal and anticlinal divisions of the original quadrants which occupy corresponding positions. The accompanying diagram gives a schematic representation of the process as we imagine it. Obviously it does not pretend to give more than a logical or symbolic presentation of the phenomena. If such a system of segregation is actually formed at the apex, it must be supposed that the axes of the system revolve with the generating spiral. Whatever hypothesis be assumed the following points remain for consideration.

1. We are as yet unable to imagine any simple system by which the four original quadrants can be formed by two *similar* divisions. Evidently there must be two cell-divisions, and if in one of them we suppose *AB* to separate from *ab*, we cannot then represent the formation of *Ab* and *aB*. Therefore we are almost compelled to suppose that the original zygotic cell forms two similar halves, each *AaBb*, and that the next division passes differently through each of these two halves, in the one half separating *AB* from *ab*, and in the other half separating *Ab* from *aB*. The formation of these four quadrants must take place in every case in which there is segregation in respect of two pairs of factors. (For three pairs there must similarly be eight segments, and so on.) The *axes* of this system may well be determined by the position of the constituent parental gametes. Reduplication or proliferation resulting in $n - 1$ gametes may then take place in

either of the opposite pairs of quadrants according to the parental composition.

2. If in the gametes of any plant some factors are distributed according to one of the reduplicated series and other factors according to the normal Mendelian system—as we know they may be—the

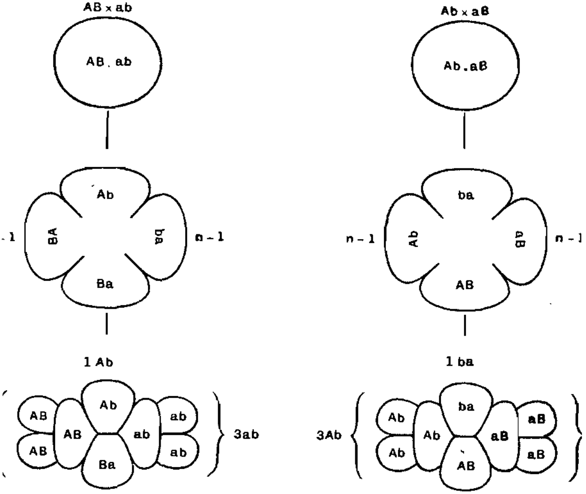


Fig. 4.

segregations by which such a system is brought about *cannot* have happened simultaneously. Moreover if various reduplications can take place very early in some individuals and not in others, we cannot imagine how the normal form of the plant remains unchanged, unless these reduplications affect tissues originally set apart as germinal.

As possibly significant we note here the fact that in the embryonic development of plants the order of the various divisions is known to be subject to great variation and it is not inconceivable that such

disturbances of the order in which the planes of division occur may indicate variations in the process of segregation[1].

3. We do not yet know whether independent reduplicated systems can be formed in the same individual. In the sweet pea for instance we have not yet seen the consequences of combining blue, erect standard, and long pollen with the fertile-sterile, dark-light axil series, and much may be discovered when such families come to be examined.

Animals

The phenomena seen in animals may well be produced by the segmentations in which the parts of the ovary or testis are determined. Hitherto no case of *coupling* has been found in animals. Among the phenomena of repulsion, however, of which many examples exist, certain suspicious cases have been observed which may mean that in animals reduplicated systems exist like those of the plants. Nevertheless at present it seems not impossible that the two forms of life are really distinguished from each other in these respects.

Terminology

Lastly, in view of what we now know, it is obvious that the terms "coupling" and "repulsion" are misnomers. "Coupling" was first introduced to denote the association of special factors, while "repulsion" was used to describe dissociation of special factors. Now that both phenomena are seen to be caused not by any association or dissociation, but by the development of certain *cells* in excess, those expressions must lapse. It is likely that terms indicative of differential multiplication or proliferation will be most appropriate. At the present stage of the inquiry we hesitate to suggest such terms, but the various systems may conveniently be referred to as examples of *reduplication*, by whatever means the numerical composition of the gametic series may be produced.

[1] See Coulter and Chamberlain, *Morphology of Angiosperms*, 1903, p. 187.

EXPLANATION OF PLATE I

Fig. 1. Photograph of the flowering stalks of two cretins. The flowers are here as fully opened as they usually become in this variety, and they are represented slightly smaller than natural size.

Fig. 2. Flower of cretin which has larger petals than usual. The standard however is not elevated and the straight stigma protrudes beyond the rest of the flower.

Fig. 3. In the centre two flowers from a cretin in which the standards are fully elevated. On the right are two other mature flowers from the same plant showing petals of the usual cretin form. On the left are two old buds.

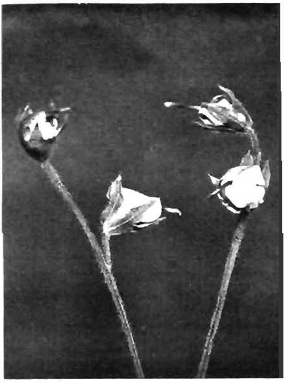


Fig. 1.

Fig. 2.

Fig. 3.

ON THE INTERRELATIONS OF GENETIC FACTORS

[*Proceedings of the Royal Society*, B, LXXXIV, 1911]

THE nature and bearing of the observations to be recorded in this paper will best be explained by tracing the steps by which they have been reached.

Early in the investigation of heredity in the sweet pea it was observed that when plants were heterozygous for two separate pairs of allelomorphs the distribution of the factors concerned was in certain cases disturbed in definite ways, such that particular combinations occurred in the gametes with greater frequency than others.

(1) The first case noticed was that of F_1 plants heterozygous for *blue* and *red* colour, and for *long* and *round* pollen. In the F_2 generation all possible combinations were represented, but the blues were for the most part long-pollened and the reds were for the most part round-pollened.

(2) The next case observed was that of F_1 plants heterozygous for *dark* and *light* axils on the one hand, and for *fertile* and *sterile* anthers on the other. In this F_2 also all combinations occurred, but nearly all the dark-axil plants had fertile anthers, while nearly all the light-axilled plants had sterile anthers.

(3) The next step was made by a study of the F_2 from plants heterozygous for *blue* and *red* flowers and for *erect* and *hooded* standards. Here it was found that one of the possible combinations did not exist in F_2, for though the blues might be either erect or hooded, the reds were *all* erect.

Examining these occurrences in the light of the presence-and-absence theory, it was clear that the phenomenon presented by cases (1) and (2) was entirely distinct from that presented by case (3). For whereas in (1) and (2) there was excess of gametes bearing the two factors over those bearing one of the other alone, the condition produced in (3) could only be obtained by a distribution such that no gamete could carry *both* positive factors. We were therefore led to recognise—

A. A system of partial *coupling* under which two factors are generally associated.

B. A system of complete *repulsion* (or as we have sometimes called

t, "spurious allelomorphism") under which two factors are never associated in the same gamete.

The partial coupling was next shown to be approximately in case (1)

$$7BL : 1Bl : 1bL : 7bl,$$

where B is blue and L is long pollen[1];
and in case (2) to be

$$15DF : 1Df : 1dF : 15df,$$

where D is dark axil and F is fertile anthers.

(4) At this stage, investigation of the properties of the exceptional members of the F_2 series was begun. In particular, the combination dark axil with sterile anthers (Df) was crossed with a light-axilled plant having normal anthers (dF). The F_2 generation from this cross was, to our surprise, a series in which *all the sterile plants had dark axils*. Here, therefore, there had been a repulsion between the same two factors which had been coupled in case (2).

In considering what could have determined this difference in behaviour, it seemed possible that the distinction might have been due to the way in which the factors had been combined in the original parents, for we knew that in the cases where coupling had resulted, the two dominant factors had been introduced together from the same parent, whereas in this new case one had come from each parent.

For several years this conjecture has been made the subject of elaborate tests, and its correctness has now been completely substantiated in several examples. Expressed in a general form, the conclusion to which we have been led is that if A, a, and B, b, are two allelomorphic pairs subject to coupling and repulsion, the factors A and B will repel each other in the gametogenesis of the double heterozygote resulting from the union

$$Ab \times aB,$$

but will be coupled in the gametogenesis of the double heterozygote resulting from the union

$$AB \times ab.$$

The F_1 heterozygote is ostensibly identical in the two cases, but its offspring reveals the distinction. We have as yet no probable

[1] There are indications that this distribution may be liable to disturbance by other factors in a way not yet understood (*Roy. Soc. Evol. Com. Rep.* IV, pp. 11–13).

surmise to offer as to the essential nature of this distinction, and all that can yet be said is that in these special cases the distribution of the characters in the heterozygote is affected by the distribution in the original pure parents.

In F_2, from a system in which A and B are coupled, almost all the offspring in the form $AaBb$ will be again built up from AB and ab gametes, so that they will again exhibit coupling; but a very small proportion will be formed from the comparatively rare gametes aB and Ab. Such heterozygotes will probably show repulsion in their gametogenesis. They must, however, be so rare (only 2 in 256, for example, from the system $7AB : 1aB : 1Ab : 7ab$) that it is almost hopeless to look for them in practice.

We know, moreover, that these phenomena are not peculiar to the sweet pea, but that they must exemplify widespread principles of genetic physiology. Repulsion has been found between the factor for femaleness and several factors of various kinds in animals—*e.g.* in *Abraxas grossulariata*; in the canary; in the fowl for at least three factors—*i.e.* (1) the factor which inhibits the development of the peculiar mesoblastic pigment of the Silky, (2) the dominant "silver" of Assendelvers (Hagedoorn) and of Sebrights (ourselves, unpublished), (3) the barring factor of Plymouth Rocks (Spillman; Pearl). Coupling till recently had been observed in the sweet pea only. Now we have the additional examples published simultaneously with this note, namely, tendrils and round seed in *Pisum* (de Vilmorin and Bateson), and short style and magenta colour in *Primula sinensis* (Gregory). In addition to these cases of coupling, Gregory also contributes a new example of repulsion, between green stigma and the factor which diminishes the stem-colour. There is thus good reason to believe that these phenomena are of no restricted occurrence in nature.

In work already published we have shown that coupling occurs according to the systems

$$7AB : 1aB : 1Ab : 7ab$$

and

$$15AB : 1aB : 1Ab : 15ab.$$

Such systems pointed to the existence of others which could be given by the expression

$$3n^2 - (2n - 1) : 2n - 1 : 2n - 1 : n^2 - (2n - 1),$$

where n is half the number of gametes needed to express the whole system.

Two more of the systems thus contemplated as possibilities have been discovered. The cases now stand thus:

3 : 1. No case yet known.
7 : 1. *Sweet Pea*. Blue factor and long pollen.
7 : 1. *Primula sinensis*. Magenta colour and short style.
15 : 1. *Sweet Pea*. Fertile anthers and dark axils.
31 : 1. No case yet known.
63 : 1. *Pisum*. Development of tendrils and round seed.
127 : 1. *Sweet Pea*. Blue factor and erect standard.

For all of these except the *Pisum* case (as yet untried) repulsion is also proved to occur. We know also that repulsion occurs between long pollen and the erect standard in families where blues are not present, but hitherto we have not had an opportunity of determining the system of coupling followed by this pair of factors.

Several curious and important lines of inquiry are thus opened up. As to the actual meaning or nature of coupling or repulsion there is no clue. The fact, however, that the mode in which factors are combined in the original parents can influence the distribution of the factors among the gametes of F_1 introduces a new conception into genetic physiology. Reciprocal matings give identical results, so no mere question of maternal influence is involved.

In attempting to form any conception of what actually happens in coupling or repulsion, and of the cause which determines that the one phenomenon or the other shall occur, we are met at once by the difficulty that we do not yet know how or when the system

$$1AB : 1aB : 1Ab : 1ab,$$

which we regard as the normal distribution for two pairs of allelomorphs, is produced. There is as yet no proof that the segregation of both pairs of factors occurs at one division, or that that division is one of those which we regard as specially concerned in maturation. Now that we know of a series involving as many as 256 terms $(127 + 1 + 1 + 127)$ it is most difficult to conceive that such a system can be produced in the maturation-divisions of the ovarian tissue of such a plant as a sweet pea. We may well be tempted to look much earlier in the developmental processes for the establishment of these differentiations, and it is not impossible that they may be established as early as the embryonic constitution of the subepidermal layer itself. As is known, this layer is—in most higher plants, at least—the exclusive source of the germ cells, a fact which

leads to those remarkable consequences which Baur has discovered in the genetics of variegated plants. Remote as this possibility admittedly is, in a problem of such extreme difficulty even improbable suggestions are worthy of consideration.

If we knew how the normal distribution, $1AB$, $1aB$, $1Ab$, $1ab$, is brought about we migbt surmise by what modification the other distributions are created. As it is, we can only say that in repulsion the heterozygote $AaBb$ gives off germ cells of two types, Ab and aB, whereas in a coupled system there are four types, AB, Ab, aB, ab, the two terms AB and ab being represented 7 times, 15 times, etc. One step further may perhaps be gained by arranging the symbols so as to represent the combinations more accurately to the eye—

$$1.\ Ab \times aB. \qquad\qquad 2.\ AB \times ab.$$
$$|\qquad\qquad\qquad\qquad |$$
$$Ab\ .\ aB. \qquad\qquad AB\ .\ ab.$$

The heterozygote $Ab.aB$ forms only two types of gametes, and the heterozygote $AB.ab$ gives the coupled series of four types. Since tbe same factors are involved in both cases it looks possible that the difference in behaviour may be a consequence of the difference in the geometrical positions of the factors relative to the planes of some critical division or divisions in the two cases. There may, in fact, be a difference of polarity between the two kinds of heterozygote.

The increase in number of the two types of cell, AB and ab, may be reached by proliferation of the two primordial cells of those two types. It may furtber be remarked that though the numbers characteristic of coupled systems cannot be produced by simple dichotomies, they can readily be represented as produced by a series of periclinal and anticlinal divisions. For example, if AB^1 by periclinal division give off AB^2, and this by anticlinal division become two cells, which again divide periclinally and anticlinally, seven cells AB are formed; by repetition of the same processes 15 are formed, and so on.

Systems of three Factors. From the list given above it will be seen that in the sweet pea we know two distinct factors, viz. erect standard and long pollen, which may be severally coupled with a third factor, that for blue colour. Here, therefore, we meet a system of interrelationship between *three* pairs, and special interest must attach to a determination of the genetic properties of plants heterozygous for all three. (The distribution of tbe factors for fertile anthers and dark axils, so far as evidence goes, is independent of this system of three pairs, so that, for the present, fertility of anthers and axil-colour can be left out of account in a consideration of the triple system.)

A plant heterozygous for B (blue), L (long pollen), and E (erect standard), can be made by any of four possible combinations.

(1) $EBL \times ebl$.
(2) $EBl \times ebL$.
(3) $Ebl \times eBL$.
(4) $eBl \times EbL$.

All these various types of combinations are now either made or being made, but as yet we are only able to give the result in the case of No. 3. In it B and E repel, and B is coupled with L on the 7 : 1 system. The coupling of B with L, since they come in together, may seem to be what the general trend of the evidence leads us to expect, but the fact that E is repelled by B rather than by L is worthy of special notice, for we know that E and L repel each other when B is not present. It suggests that there must be an "order of precedence" among the factors composing such a system, and the suggestion is plausible that this order will follow the grade of coupling in which the factors are accustomed to be linked.

It will be observed that, given a system under which a pair of factors are coupled, it is possible to produce the system under which the same pair repel each other. For all that is necessary is to breed together the rarer terms of the coupled series, viz. Ab and aB.

From the repelling system, on the contrary, in the absence of a fresh variation, we have no obvious way of constructing the coupled system. This consideration has an obvious application to those cases in which *sex* operates as a repelling factor. In the fowl, the canary, and *Abraxas grossulariata*, femaleness thus acts as a repelling factor against various elements determining pigmentation: and our experience of the plants leads us to suppose that if the factors involved could be built up in the right combinations, femaleness might be coupled with the factors it now repels.

Extraordinary consequences, both to the distribution of the sexes, to the distribution of factors between them, and perhaps to the causation of fertility, must be anticipated if this condition could be fulfilled. There may be an indirect way of actually accomplishing these results. For, seeing that sex in the fowl acts as a repeller of at least three other factors, when birds are built up so as to be heterozygous for several of these, some of them may be found able to take precedence of the others in such a way as to annul the present repulsions, with subsequent coupling as a consequence.

A CASE OF GAMETIC COUPLING IN *PISUM*

[*Proceedings of the Royal Society*, B, LXXXIV, 1911]

For some years past a variety of culinary peas has been grown at Verrières-le-Buisson, remarkable for the fact that it has no tendrils, each of the normal tendrils being represented by a leaflet. The figure shows the appearance of the leaves of this variety, with leaves of normal plants for comparison.

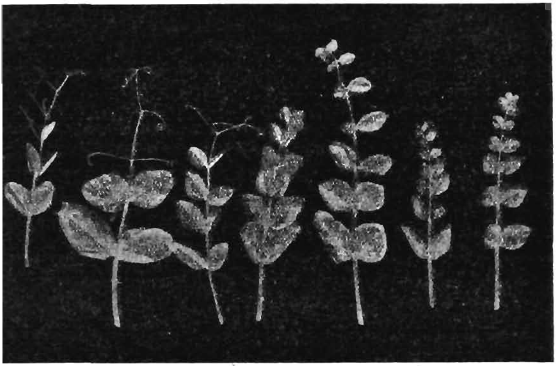


Fig. 1. The four right-hand leaves are from "Acacia" peas; the three left-hand leaves are from normal plants. The figure on extreme left shows a leaflet with a tendril opposite to it. Such asymmetries are common in the normal types.

These "Acacia" peas, as they are called, breed perfectly true. Their origin is unknown. The variety has wrinkled seeds.

Crosses were made at Verrières between the Acacias and a variety having normal tendrils and round seeds. The tendrilled character was fully dominant in F_1, which, of course, bore both round and wrinkled seeds. When these seeds were separately sown it was observed that the round seeds gave rise almost exclusively to tendrilled plants, and the wrinkled seeds almost conclusively to Acacias, though there were a few exceptions each way.

As the case was almost certainly one of gametic coupling between roundness of seed, and tendrils, the problem was clearly worth minute investigation, and a quantity of material was transferred to the John Innes Horticultural Institution, Merton, Surrey, for this purpose. The offspring of two F_2 plants, heterozygous in both respects, were, in particular, the subject of study.

Unfortunately, the distinction between rounds and wrinkleds was in these families not perfectly sharp, and much irregular pitting occurred. When the plants grown from these seeds were harvested it was found that errors in sorting had been made both ways, one seed having been sown for a round which gave rise to a plant with exclusively wrinkled seeds, and two seeds which had been sown as wrinkled proved to have been heterozygous rounds. The earlier counts had therefore to be rejected, and in order to obtain perfectly reliable numbers it was clearly necessary that the nature of the starch in each seed should be separately determined for each seed before it was sown. As Gregory[1] had observed, by microscopical examination of the starch grains, this discrimination may be made without difficulty.

The microscopical test was applied by Miss C. Pellew, Minor Student of the Institution, to F_1 seeds of heterozygous plants on a considerable scale, and the seeds were then sown. Only a fragment of a cotyledon need be removed for testing, and the seeds germinated perfectly after the operation. The results were as follows:

	Round		Wrinkled	
	Tendrilled	Acacia	Tendrilled	Acacia
Observed	319	4	3	123
Calculated on a coupling of 63 : 1	*333*	*3·4*	*3·4*	*109*

These figures leave no reasonable doubt that the system of gametic coupling followed in this case is

$$63TR : 1Tr : 1tR : 63tr,$$

where T is tendrilled, and R is round seed. This gametic system gives the zygotic ratio

$$12161TR : 127Tr : 127tR : 3969tr = 16384,$$

from which the above calculation is made. This particular system has not been hitherto encountered, but it is, of course, one of those contemplated by the general expression for coupled systems.

There is no difficulty in distinguishing the tendrilled from the

[1] *New Phytologist*, II, 1903, p. 226.

acacia plants when six to seven leaves are developed, but in some of the tendrilled—doubtless the heterozygotes—the apical tendril is sometimes strap-shaped, especially in the youngest tendril-bearing leaves.

On one occasion at Verrières, Acacias came in a strain of Sandar's Marrow. Though natural cross-fertilisation is extremely rare among peas (much rarer than in sweet peas) we can hardly douht that these Acacias were recessives extracted after an accidental cross with the pure strain growing in the same garden. Both among various peas grown at Verrières, at Reading, and at Grantchester, a few unquestionable examples of crossing have been observed since critical attention has heen devoted to the study of heredity in peas. The crossing is probably effected by visits of *Megachile* to flowers in which for some reason their own pollen has been inoperative.

In the case of the derivatives from the Sandar's Marrow strain the occurrence of strap-shaped tendrils, presumably on the heterozygotes, has been often observed, and some plants have many such intermediate tendrils.

The original cross which gave coupling between T and R was in the form $TR \times tr$. Experiments are now in progress for testing whether when a cross is made in the form $Tr \times tR$ the gametogenesis of F_1 will show repulsion of T from R, and on the analogy of what has been seen in sweet pea and in *Primula sinensis* this result may be confidently anticipated.

Whether any similar interrelation exists between the tendril factor and factors other than that for round seed cannot be yet stated, but it is practically certain that the factors for yellow seed and for tall stem do not stand in any such special relation to it. The case is also interesting inasmuch as it is the first yet met with in which neither of the coupled factors is in any way concerned in determining pigmentation.

In conclusion it may be remarked that an identical "acacia" variety exists in the sweet pea, and its properties are also under investigation. In the sweet pea, however, there is no variety with truly wrinkled seed. The types with self-coloured lavender flowers have somewhat shrivelled seeds, but the starch of these is normal.

HEREDITY[1]

[British Medical Journal, 1913]

LET me on behalf of my colleagues, the students of genetics, express our deep sense of the honour conferred upon us by the organisation of your Congress in choosing our science as the subject of one of the general addresses. It is scarcely necessary that I should say, on my own behalf, that I feel it an extraordinary privilege to he permitted to represent that science on such an occasion.

This is a great privilege, but it entails also a very grave responsibility. Conscious as we are of the exceptional significance that the study of heredity must before long assume, it would be mere affectation were I to suggest any misgiving as to the propriety of allotting to this subject a conspicuous position in your deliberations. To the penetrative foresight of Francis Galton it was evident long ago that these aspects of physiology must one day become one of the chief preoccupations of reflecting minds. That inference he drew from a broad contemplation of the facts of descent. Traces of order among these phenomena he did indeed perceive, and by great labour and ingenuity he even gave numerical expression to his conclusions. But great as his services were in attracting attention to the problem, no one before the rediscovery of Mendel's work had ventured to imagine that the confusion, the paradoxes, the capricious disorder of the phenomena of descent were, in very great measure, capable of a simple and ready analysis. It is this knowledge which has given to genetic science a position paramount among the branches of physiology, showing that in accurate genetic analysis a means is given not merely of elucidating the interrelations of parent and offspring—the immediate subject of our investigations—but of contributing also to a right interpretation of various special problems of pathology and of anthropology, perhaps, also, to a true understanding of the course of human history, and certainly to the direction and control of the destinies of mankind. Knowing, as I must, that the manner in which these issues are presented to you to-day cannot fail to influence in some measure the development of genetic study in the medical world, I should be insensitive did I not feel how responsible is the position I now occupy. Most of all I fear that I may seem in some degree to exaggerate not the importance of the principles already ascertained,

[1] Address delivered at the Seventeenth International Congress of Medicine, London, 1913.

but the precision with which they can be shown to apply in the special cases of human physiology. In all the arts, perhaps most in the art of exposition, the hardest thing is to simplify the presentation by the omission of detail, and at the same time to leave the picture true to natural fact. So let me, therefore, at the outset say that in regard to almost every instance of principle I shall bring before you, though rule may be perceived, we have evidence of exceptions also. This is true even of the rules traced by minute analysis in the plants and animals amenable to experiment, and necessarily far more true of the human phenomena which are brought within our reach for the most part by imperfect records. As in every department of physiological advance, we have first to trace the course of those great sweeping curves which lead to the recognition of ascertained law, and later those minor deviations, perhaps equally significant, which must hereafter be the subject of a further analysis.

Now the essence of Mendelian principle is very easily expressed. It is, first, that in great measure the properties of organisms are due to the presence of distinct, detachable elements, separately transmitted in heredity; and secondly, that the parent cannot pass on to offspring an element—and consequently the corresponding property—which it does not itself possess. The determination or recognition of these elements by analytical breeding is one of the main objects of present-day genetic research. Each germ cell, ovum or sperm, may contain or be devoid of any of these elements, and since all ordinary animals and plants arise by the union of two germ cells in fertilisation, each resulting individual may obviously receive in fertilisation similar elements from both parents or from neither. In these cases the offspring is "pure"-bred for the *presence* of the character in question, or for its *absence*. But it may be formed by the union of dissimilar germs, one containing the element, the other devoid of it, and in this case we call the individual cross-bred, or heterozygous in that respect.

A population thus consists of three classes of individuals—those pure for the presence, having received two doses, of an element; those pure for the absence of the element, having received none of it; and the cross-breds, which have received one dose only.

From the physiological standpoint it is of great importance to distinguish the positive from the negative characteristic. But since it often happens that the full effect is produced in the organism by one dose only of a character, we have felt justified in regarding this

positive effect as the sign or proof that it is caused by something present. A plant, for example, though cross-bred for tallness, may be as tall as one pure-bred for tallness.

Each dwarf plant, whatever be its parentage, can only produce dwarf offspring. Not having tallness, it cannot transmit that property. A cross-bred *tall* plant can, by self-fertilisation, produce both tall and dwarf offspring. Fowls with silky feathers cannot, if bred together, have offspring with normal featbers; but two birds, normal to all appearance, can, if they be cross-bred in that respect, produce silky offspring.

At a later stage we will consider to what extent we are justified in thus discriminating between the positive and the negative characters, but for the present we will note that, as a matter of symbolical expression, the distinction is immaterial. Now the organism produces germ cells representing in equal number the several characteristics of the germ cells from which it arose. There is, as we call it, *segregation* between the elements introduced from the parent. The double structure of the soma is, when the germ cells are sound, resolved into the single structures of the germ cells. If the organism is pure-bred in any respect, all its germ cells are alike in that respect. If it is cross-bred, its germ cells represent in equal numbers the positive or negative characters which were brought together in fertilisation. In consequence, the numbers of individuals resulting from the various possible forms of union follow regular arithmetical rules, and the proportions in which the several classes appear give us the means of tracing and identifying the various systems of descent.

It was naturally with great interest that we began the examination of human pedigrees, and the result of that search soon showed that many of the more definite hereditary diseases and malformations follow one or other of the systems with which Mendelian analysis has familiarised us. The first condition thus recognised to have a simple Mendelian inheritance was the peculiar malformation known as brachydactyly, described in America by Farabee. Another example is congenital cataract, studied by Nettleship, to whose admirable researches we owe many of our most valuable and instructive pedigrees. Both these conditions descend as dominants. It is cbaracteristic of them that unaffected members of the families do not transmit. Not having in them the critical element which causes the condition, they cannot pass it on to their posterity. In the human examples the individuals affected are almost always heterozygous, and hence

among the children which are born to their marriages with normal persons, we expect the affected and unaffected to be in equal numbers.

Since then such pedigrees have been recognised in abundance. The collection of such evidence we owe especially to Nettleship, Gossage, Drinkwater, Lundborg, Weil, Bulloch, and many more.

Some of these, which may be stated with fair confidence to descend commonly as dominants, are the following:

Brachydactyly; claw-shaped extremities; cartilaginous exostoses; membranous cranio-cleido-dysostosis; hypoplasia of the teeth; diabetes insipidus; chronic trophœdema (generally).

Skin affections.—Tylosis, epidermolysis bullosa, telangiectasis, hypotrichosis, porokeratosis, xanthoma.

Ophthalmic diseases.—Presenile cataract, ectopia lentis (sometimes), coloboma (sometimes), distichiasis, night-blindness (certain forms), retinitis pigmentosa (sometimes).

Nervous diseases.—Angeio-neurotic œdema, tremor hereditarius, ptosis, Huntingdon's chorea, and probably several of the forms of spastic paralysis and of myatrophy.

Respecting nearly all these it may be remarked that exceptional cases, some undoubtedly authentic, are on record in which affected children have been born to parents actually or apparently normal. Many of these exceptions are undoubtedly genuine and serious, but others may be ascribed to irregularities in the age of incidence, and to mistakes as to slight cases.

Another difficulty arises from the fact that the numbers are frequently irregular. This is in part caused hy imperfection in the records. In part, however, I think these aberrations point to real peculiarities in the process of segregation. We know well that in certain plants like wheat and peas the expected numbers appear with great constancy, but in others, as stocks and the primulas, long "runs" are so common that smooth results are only obtained by the summation of large series of observations. We are perhaps right in conceiving the germinal tissue of a heterozygote as an emulsion of the two types, sometimes coarse, sometimes fine, and the degree of smoothness of the results may be an indication of its state in this respect.

In regard to the large group of diseases of nervous origin, such as Friedreich's disease, Thomsen's disease, and others, these sources of difficulty are especially serious; and though from study of many genealogies I have come to the conclusion that most of them are essentially dominants, I offer this opinion with reserve.

Of recessive conditions in man we have less abundant evidence. Inasmuch as they usually appear from the unions of parents both apparently normal, though heterozygous for the condition, their occurrence is rare and sporadic. Lundborg has shown with great probability that paralysis agitans is one of these. The constant intermarriage of families in the valleys of Sweden, Norway, and the Alps gives the best opportunity for the study of this form of descent. Lately, also, the American students of genetics have produced evidence making it clear that feeble-mindedness has at least one of the marked features of a recessive condition. When both parents are feeble-minded they have no normal children. It is nevertheless difficult to regard this condition as a simple recessive, for unions of the feeble-minded with normal persons almost always produce some feeble-minded children. Among our experimental families of plants and animals there are mysterious examples somewhat comparable with those, but the exact nature of the complication is still obscure.

Other conditions which exhibit a behaviour characteristic of recessives are albinism, myoclonus epilepsy, and alkaptonuria. They may all appear in the children of normal persons, with special frequency as the result of marriages of related parents, and there can be no reasonable doubt that these conditions are due to the loss of some factor present in normal persons.

At this stage attention should be called to a remarkable group of cases in which the appearance of abnormality may almost without doubt be regarded as partially dependent on the conditions to which the soma is subjected. Of these, I may mention in particular some of the congenital abnormalities, such as hallux valgus, and some of the congenital deformities of the joints, as, for example, dislocation of the hip or of the radius. In these cases we meet the curious fact that whereas the condition most usually appears in the offspring of normal parents, it may, in certain families, be transmitted from parent to offspring as a dominant. I am inclined to compare these phenomena with those so often witnessed in incubating eggs. When the incubators are not running uniformly, many of the chickens are born with deformed feet. Such abnormality, however, is found with especial frequency in particular strains of birds, though eggs from other strains exposed to the same conditions may give perfectly normal results. The liability is the thing transmitted, but without the appropriate conditions the effect is not produced.

The next group of cases to which I would call your attention is one

in which the descent of the abnormality is limited wholly or partially by sex. Of these, the best known examples are those of the descent of colour-blindness, hæmophilia, and one of the forms of nystagmus.

In regard to colour-blindness, the fact has long been known that males are affected with exceptional frequency. Colour-blindness among women is decidedly rare. Horner was, I think, the first to call attention to the fact that in the pedigrees of this condition there is remarkable regularity. Normal women transmit the affection to their sons, whereas colour-blind males with rare exceptions have only normal offspring. It is possible to interpret these phenomena by the suggestion to which several of us inclined some years ago, that colour-blindness is a dominant, inasmuch as the normal males cannot transmit it. We were led to regard the condition as due to the presence of something inhibiting normal colour sense rather than to the absence of the factor to which that sense is due. Further investigation has, however, thrown doubt on this simple explanation. As to the descent, however, there is no doubt that the sons of colour-blind males do not inherit the peculiarity, and therefore cannot transmit it. The daughters of colour-blind fathers inherit it, and though it does not appear in them, probably all of them have the power of transmitting it to their sons. Knowledge derived from direct experimental breeding of various animals has provided a very remarkable scheme by which this course of descent can be represented factorially. One of the simplest of such examples is that of the inheritance of colour in Sebright bantams. When a cross is made between a golden hen and a silver cock, all the chickens come silver, but when a reciprocal cross is made, a silver hen being mated with a golden cock, the pullets come golden but the cockerels come silver. In this case we must regard the silver as dependent on the presence of a dominant factor, and the golden as due to its absence. The silver male is pure for silver, *SS*, having received that factor from both parents, but no pure silver hen exists. The hen is heterozygous for silver, and may be represented as *Ss*. We must further regard the hen as also heterozygous for femaleness, *Ff*. In the formation of the eggs there is what we call repulsion between the factor *F* and the factor *S*; the two are not present together in any egg. Those eggs which are destined to become males carry factor *S*, and those eggs which are destined to become females carry factor *F*. Now in colour-blindness, the repulsion that has been so clearly proved between these factors may be represented as acting in the germ cells of the male between the factor for maleness

and the factor for colour-blindness; such that the sperms destined to become males carry factor M, but do not carry the factor for colour-blindness, which passes entirely into those sperms which are destined to produce femaleness. It is evident that females heterozygous for colour-blindness are not colour-blind, and that colour-blind females can only be produced by the meeting of two germ cells both bearing the affection.

It follows from the hypothesis that the sons of colour-blind women will all be colour-blind, and all the records of such families with which I am acquainted, with a single doubtful exception, are in agreement, in that the sons of such women were all colour-blind.

It is practically certain that the same system of descent sometimes holds for nystagmus, respecting which Nettleship has recently collected some important genealogies.

As to the other sex-limited conditions in man, I can only say a few words. Hæmophilia is the most familiarly known of these. It is likely that the condition in men follows the same descent as that established in the cases of colour-blindness, but inasmuch as males affected with the condition very rarely live to the age of puberty, little is known of their powers of transmission.

I have already spoken of night-blindness as a condition which descends as a dominant, but it is very interesting that Nettleship has lately published certain pedigrees of night-blindness in which the descent is of the sex-limited type. This particular night-blindness is apparently associated always with a high degree of myopia, and I suppose there can be little doubt that the recognition of the genetic distinction will lead to the discrimination of pathological differences also. Pseudo-hypertrophic muscular paralysis is another condition which descends in a similar way, and at least one large pedigree has been compiled by Herringham showing the same descent for peroneal atrophy.

At an earlier stage of this lecture I mentioned a doubt as to the justice of the inference that the characteristics which behave as dominants are due to the *presence* of factors, and to that point I must now return. In our experimental studies of animals and plants we are aware that certain negative characteristics may be produced not by the absence of a quality, but by the presence of some factor which inhibits its expression.

In illustration I may show you an example in the Chinese primrose. These plants may have their flowers coloured or white and we are

aware that the white may owe their whiteness in certain cases to the absence of colour; in which case, of a cross with the coloured form, the offspring are all coloured, whereas other whites contain something which destroys or inhibits the development of the pigment which is contained in them, and when such whites are crossed with coloured the offspring are white or nearly so.

In view of these examples the question fairly arises whether some of the dominants whose descent I have traced in human pedigrees may not in reality be due to the absence of some factor which in normal persons prevents such development. This suggestion was prominently brought forward by Doncaster in regard to colour-blindness. He lately suggested a scheme according to which we should regard all normal males of the population as heterozygous *Nn* for a factor *N* normality, and all ordinary females as homozygous *NN* for the same factor. In either case the course of the descent would, both qualitatively and numerically, be the same as that represented by the earlier scheme. Between these two methods of representation we cannot as yet distinguish. The point is of great importance in another respect. The question will be prominent in most of your *minds, whence do these dominant factors come? Whereas it is com*paratively easy to conceive some process by which some elements of the composition may be lost, we are quite unable to suggest any source from which a factor may be derived or any mode by which it may be taken into the genetic system of the organism. We have been accustomed to speak of factors as being added to or subtracted from the sum total of an individual composition, but as to the actual origin of new dominants there is very little contemporary evidence.

In the case of those animals, such as the fowl, the wild original of which we think we know, many factors exist in our domesticated breeds which are not possessed by any of the wild species. No wild species, for example, has the complicated combs that we know in our domesticated breeds. None has the dominant white colour of the Leghorn, and many other such instances might be given. How have these elements been added to the composition of the fowl? The problem is exactly parallel to that constituted by the occurrence of brachydactyly or night-blindness in man. We can only trace back these peculiarities to a single individual of whose origin nothing is known, but whence did he derive the factor to which he owes his *peculiarity?*

We may compare these cases with those of the origin of an infectious

disease, such as typhoid fever. When a medical officer of health recognises typhoid in his district he knows that it must have come from some definite source of infection, and but for one feature in the descent of dominants we might be tempted to suggest that they also arose through the introduction of some element from without into the system. I see no *à priori* impossibility in such a belief, but in these dominants we know that the distribution among the germ cells is approximately symmetrical, and nothing that we know of animals and plants justifies the suggestion that a foreign element can be so treated in gametogenesis. Perverse as such a suggestion may appear, I do not think we should close our minds to the possibility that these dominants arise by a process of loss of some inhibiting factor. Until we have some far more direct method of recognising the presence of factors this suggestion cannot be positively gainsaid.

Let me call your attention also to the inference which this suggestion would have on the conception of evolution. We might extend the same reasoning to all cases of genetic variation, and thus conceive of all alike as due to loss of elements present in the original complex. For all practical purposes of symbolic expression we can still continue to use in our analyses the modes of representation hitherto adopted, but we must not, merely on the ground of apparent perversity, refuse to admit that the lines of argument here indicated may prove sound.

Much as we now know of the inheritance of these abnormalities—some common, others rare—we know little of the descent of the normal characteristics of an ordinary human population. Indeed the only normal characteristics as to the genetic nature of which we have clear evidence, are the colour of the iris and, to some extent, the colour of the hair. Our knowledge of these is derived from the work of Hurst; he it was who first succeeded in determining the inheritance of eye colour, which had long been a puzzle to anthropologists. The facts which he collected clearly showed that the presence of pigment on the front of the iris—the condition commonly known as brown or black eyes—is a dominant, whereas the absence of this pigment—the eyes we variously call grey or blue—is a recessive. And so far, though I anticipate the possibility of exceptions, no example has yet been produced of two parents critically known to have blue eyes producing offspring with brown or black eyes. As similarly shown, red hair behaves as a recessive, and I understand that at the forthcoming meeting of the British Association in Birmingham, Hurst will

arrange a demonstration of this as exemplified by the inhabitants of a Midland village.

From the records of portraits of the royal house of Hapsburg it is clear that the familiar facial characteristics of the family behave with fair regularity as a dominant, and there are indications that several of the artistic gifts follow with some accuracy the course characteristic of recessives. By careful observation and record the list might rapidly be increased.

Referring to the descent of various forms of insanity, nothing has been made out with certainty with the exceptions that I have mentioned—hereditary chorea, which behaves as a dominant, and the condition somewhat vaguely described as feeble-mindedness, which behaves as a recessive. The genetic analysis of insanity is at the present time practically impossible from the fact that the diagnosis of the various forms of insanity is by no means clear, and also from the fact that the conditions of life have obviously much to do with the development of such weaknesses.

Similar difficulties arise in regard to deaf-mutism. It is not in question that this condition is very often transmitted, but forms of deafness are so various, and there is such uncertainty as to the nature of the condition in any given case that we cannot expect to perceive the operation of any regular system here. It is not impossible, also, that in regard to the descent of liability to infectious disease, we may hereafter trace rules similar to those which have now been established in plants, especially by Biffen.

I propose now briefly to allude to some other significant aspects of these results. First as to the nature of segregation. This, I think, we must regard as a process comparable with the mechanical separation of substances which will not mix, or mix imperfectly; whereas some factors are continually transmitted in their entirety, others are liable to be broken up by what I regard as a process of quantitative fractionation occurring in the mechanical dissociation of the elements at certain critical cell-divisions. As to which are the critical cell-divisions we have no clear indication. I cannot agree with those of my colleagues who think segregation must occur exclusively in the maturation processes. The case of the double stock, in which the whole male side of the plant differs genetically from the female side, as proved by Miss Saunders, shows almost conclusively that segregation may occur in somatic divisions. It is also difficult otherwise to interpret the fact that in certain cases the parental combination influences the

distribution of factors among the gametes so that the distribution among the grandchildren is different according to the way in which the characters were combined in their grandparents. Into these details I cannot now enter.

The tendency of our work, as you will perceive, is more and more to exhibit the definiteness and fixity of the laws of descent. The medical man, justly proud of what he can do to make good bodily shortcomings, looks naturally to the conditions of life as the influences which chiefly determine destiny. The statesman, to whom physiological fact is a mystery that he rarely feels any desire to explore, inclines naturally to a similar conception of life. There are signs that more true views are beginning to prevail. It is impossible to study such pedigrees as those of night-blindness, in which a condition introduced by one individual into a community hundreds of years ago continues to be perpetuated according to definite arithmetical rules among a remote posterity, without being impressed with the fact that whatever influences may be brought to bear by hygiene or by education, the ultimate decision rests with the germ cells. Evolutionary change is effected not so much by gradual transformation of masses under ameliorating or detrimental conditions, but, in the main, by the occurrence of individual and sporadic variation.

It is beyond my province to discuss in detail the practical question denoted by the word "eugenics." Those who are engaged in the work of physiological analysis probably do well to keep clear of those distractions. The direction, however, in which genetic research points is not difficult to determine. Sir James Crichton Browne has discussed at this Congress the striking percentage increase of lunacy in recent decades, and, as always when such topics are under consideration, there are persons disposed to lay the blame on the conditions of life, the severity of the modern struggle, a greater or less consumption of alcohol or other drugs, and so forth; those, however, who have some knowledge of genetic physiology are aware that the whole force of modern science and legislation has hitherto been exercised in the preservation of defective strains in our midst, and will not feel serious hesitation as to the true cause of the increase.

The Mental Deficiency Bill we recognise as, in principle, a wise beginning of reform, but, on the other hand, we cannot hear without disquietude, of the violent measures that are being adopted in certain parts of the United States with similar objects. It is one thing to check the reproduction of hopeless defectives, but another to organise

a wholesale tampering with the structure of the population, such as will follow if any marriage not regarded by officials as eugenic is liable to prohibition. This measure, we are told, is actually proposed in certain States. Nothing yet ascertained by genetic science justifies such a course, and we may well wonder how genius and the arts will fare in a community constructed according to the ideals of State Legislatures.

Philologists tell us that, by an irony of development, the word "dull" comes from the same original which in Dutch has become "dol"—mad, and is better known to most of us in the German equivalent "toll." But I anticipate that, connected as the ideas may be, we might, by ridding our community of mania, leave it gravely infected with dullness. There are other no less obvious considerations which I might develop, but I trust I have said enough to show that in the experimental analysis of genetics we have an instrument of novel and extraordinary power, and I am not alone in foreseeing that genetic science must profoundly influence the course of human thought, and, ultimately, the conduct of society.

ON THE GENETICS OF "ROGUES" AMONG CULINARY PEAS (*PISUM SATIVUM*)

(With Plates II–VII)

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MANY, perhaps most, varieties of culinary peas (*Pisum sativum*) at present in cultivation are liable to throw "rogues" of a peculiar kind which may be described in general terms as wild and vetch-like. The proportions in which these rogues occur under commercial conditions are of course various, depending on the care with which the parent crop had been rogued, on the nature of the variety, etc. In a crop of Gradus considered fairly free from rogues we estimated the proportion at 1 per cent., but we have seen crops more nearly free from rogues and of course several much worse.

For some years we have been investigating at this Institution the genetic relations of these rogues to the typical varieties from which they come. The main problem remains unsolved and the work is still in progress, but the facts already established are so unusual that it seems desirable to make them generally known. So far as we are aware the case is as yet unique.

The term "rogue" is applied by English seed growers to any plants in a crop which do not come true to the variety sown. For example, tall plants found in a crop sown as dwarf, coloured plants in a white variety, plants with pods of a wrong shape, or in any other way differing from the standard type of the variety are called "rogues." It is the universal practice of all good seedsmen to exterminate these untrue plants every year at some stage before the crop is gathered.

When peas are grown for seed on a commercial scale it will readily be understood that untrue plants are introduced in various ways, mixture, crossing by insects, and the persistent recurrence of a recessive form being the most obvious sources of such plants. Rogues referable to these several origins we have of course seen among peas, but the facts preclude the supposition that the special rogues with which we are here concerned are introduced either by mixture or crossing, nor can they be regarded as recessives coming from a heterozygote in the ordinary sense.

Preliminary Statement of Results

By Messrs Sutton's advice we began our work in 1911 with Ne Plus Ultra (N.P.U.), Early Giant (E.G.) and Duke of Albany (D.A.). For

some unknown reason N.P.U. did badly on our land, suffering so much from bacterial disease that after 1912 we gave it up. Our observations therefore relate mainly to E.G. and D.A. These two differed considerably in the fact that whereas typical D.A. plants with us have thrown no obvious intermediates between type and rogues[1], such plants do occur in E.G. and their behaviour raises some curious problems. Our experience of all three varieties may be summarised as follows:

(*a*) *Thoroughly typical plants do occasionally throw rogues* (*E.G. and D.A.*) *and certain intermediate forms* (*E.G.*).

(*b*) *The rogues, of whatever origin, when fertile*[2], *have offspring exclusively rogues* (*N.P.U.; E.G.; D.A.*).

(*c*) *Intermediates* (*raised from types*) *showing combinations of type and rogue characters give mixed families of various compositions* (*E.G.*).

(*d*) *Crosses between types and rogues, however made, have* (*with the rare exceptions mentioned in E.G.*) *always given rogues though these in their juvenile condition are generally type-like; and these rogues have always given only rogues* (*N.P.U.; E.G.; D.A.*).

Description of Rogues

Foliar Parts

Most of the best modern forms of culinary peas have the stipules, leaflets, petals, and pods, large and broad. Among these typical plants the rogues are distinguished at once *by the smallness of their appendicular parts*. They are at least as tall as the types, generally perhaps slightly taller, but their stipules, leaflets and petals are comparatively small and narrow, though the plants are perfectly healthy and well grown. The length of the foliar parts is also reduced, but to the eye the greatest difference is in width. Probably in consequence of this diminished extension the stipules of the rogues end in a point formed by the acutely converging edges. The stipules of the types have much more obtuse, or even rounded apices, and their bases are full and bulging. The leaflets of the rogues differ similarly from those of the types. In both the midrib ends in a fine, hair-like spine. In the type this stands on an emarginate, truncated end, the curve of the leaf springing about at right angles from the spine. In the rogue the shapes of the leaves vary considerably according to their position

[1] See later, p. 251, *note*.

[2] Sterile rogues occur as rare exceptions.

on the stem. Those at the upper nodes are scarcely truncated if at all, and the sides of the leaflets converge acutely to the spine. Lower down the stem the leaflets approach more nearly to the typical shape, but are distinguishable by their less ample development. (See Pls. II and III, figs. 1–5.)

The types with which we have chiefly worked, Duke of Albany and Early Giant[1], have the foliar parts much marbled on the upper sides with white. This marbling is due to air-spaces under the epidermis. It is often developed to some extent in rogues, but never so much as in types, and in the upper leaves of the rogues it is usually not present at all.

The texture of the leaves also differs, those of the rogues being stiffer and harder, those of the types being more limp and cockled, indicating probably a want of complete correlation between the rates of growth of the several layers.

Pods

The pods contain as many seeds as those of the types, but those of rogues in E.G. and D.A. with great constancy *curve upwards along the dorsal suture.* In seeking for characters positively distinguishing these rogues the curved pod is one of the most definite and easy to recognise. There are varieties of peas having curved pods as a normal character (*e.g.* the Serpette peas, Pois d'Auvergne, and Gladstone), and it is possible that the curvature seen in these varieties is genetically of the same nature as that of the rogues; but however that may be, the curved pod is, so far as we know, always found on these rogues, though on the types from which they are derived all well-grown pods have the dorsal edges straight for most of their length[2]. These differences in shape are evidently all expressions of differences in proportional growth along the several axes, and we incline to regard them as various consequences of a deficiency of extension of the foliar parts in the rogue, but we are not able to analyse the phenomena further. (See Pls. VI and VII, figs. 10–15.)

In the rogues of E.G. and D.A. the curved pods are, as we have said, a striking feature. Attention should however be called to the circumstance that the pods of both these varieties are *pointed.* In

[1] Early Giant is the name by which Messrs Sutton designate a special strain of the well-known *Gradus.*

[2] In nearly all varieties there is a slight upward curve beginning in the peripheral quarter.

N.P.U. they are *blunt* and the pods of rogues from this variety are straight. Moreover the Serpette and other varieties normally curved have also pointed pods; and though our evidence on this question is insufficient we are inclined to regard the blunt-ended pod as incompatible with a full degree of curvature.

Seeds

In shape and colour the seeds of the types and the rogues are not distinguishable from each other, but those of the rogues are slightly smaller (see later). There is however a difference in flavour, those of the rogues, whether raw or cooked, being less sweet to the taste than those of the types. The starch grains of the two forms appear identical. Estimations have been made of the amount of sugar in type and rogue seeds, but so far no consistent difference has been discovered. Probably therefore the chemical distinction, which must certainly exist, is more profound.

Production of Rogues by the Types

At first sight it seems improbable that the thin, weed-like rogues can be actually the offspring of the luxuriant types, and we suspected the case to be one of accidental mixture. Rogues however, apart from their special features, have the characteristics of the types among which they occur. They flower at the same time whether early or late, their pods are stumpy or pointed according as the type is stumpy or pointed, and so on. But even if the rogues had arisen originally from the types or simultaneously with them, their perpetuation might be merely due to imperfect sorting[1]. This suggestion however has proved quite erroneous.

We began our experiments by grading the seeds of a commercial sample according to size. We found that the proportion of rogues is actually much smaller among the plants raised from the largest seeds. For example, 302 largest seeds from D.A. and 149 from E.G. gave no rogues; 119 from N.P.U. gave one rogue: but occasional rogues came among the plants both from the medium and the small seed samples.

[1] Certain rogues no doubt are thus perpetuated. For instance, in the case of Veitch's Perfection, a wrinkled pea believed to throw a *round*-seeded rogue, though all round seeds are carefully picked out, experiment showed that the perpetuation of the round-seeded plants was due to the fact that the seeds at the apex of the pods are often so much dimpled as to pass for type seeds, and thus escape the sorters, giving rise of course to round-seeded plants when sown.

Owing however to fluctuation in size no even approximately accurate sorting can be made in this way.

In D.A. the average weight of well-developed seeds was found to be 0·41 g. for the types (9 plants) and 0·37 g. for the rogues (5 plants). In E.G. these weights were 0·41 for the types (11 plants), and 0·34 for the rogues (23 plants)[1]. These differences are considerable, but many type seeds fall much below the rogue average and the seeds of an occasional rogue surpass the type average. In most varieties no doubt by choosing only the very finest seeds the rogues could in general be avoided, but genetic purity cannot be thus attained.

As to the production of the lower forms (*i.e.* rogues or intermediates) from the finest type plants the details are evidently different for the several varieties; and within the same variety, strains descending from different individuals differ considerably in the liability to throw rogues. *The labour of rogueing pea crops is so great that the permanent elimination of rogues would be a matter of considerable economic importance to seed-growers.* From our experience however the prospect of attaining that object in the case of the large-leaved varieties at least does not seem very good, though from the great difference between strains a relative purity may perhaps be reached.

The results of sorting the seeds led us to think that it would be possible to raise a pure strain of types. As regards E.G., though of the typical plants raised from the largest seeds some gave families exclusively typical, others threw occasional plants of the lower classes. For example, a type-plant in 1911 gave a family (about 60 plants) in 1912 all types. In 1913 from these were raised 15 families. Some of them contained rogues, but one large family was free from them. From that family in 1914 we raised 29 families, of which 22, aggregating 1122 plants, were all types. The remaining 7 families each contained a single aberrant plant, the total being 357 types and 7 aberrants; or 51 : 1. This is the strain of E.G. which has thrown fewest rogues. Where the proportion of aberrants is so small it is evidently impossible to be confident that plants which give even 100 offspring all typical were incapable of throwing rogues.

In the case of D.A. a much nearer approximation to purity was made. From selected type plants in 1911 about 3300 plants were raised in 1912, all typical. From selected plants among these about 12,000 were raised in 1913, and no aberrant individual was found

[1] The intermediate plants, spoken of later as class 3, gave an intermediate weight, averaging 0·37 g. (11 plants).

among them. In dealing with these large numbers of plants it will be understood that the characters of every single plant cannot be positively guaranteed under the conditions of the experiment, for in all such crops there are some plants that have not grown well and might conceivably be aberrant, but we have confidence that no well-grown plant departed from that type, and only the finest plants were used as parents. From eight well-grown families in 1913 (containing, as we have said, no rogues) the seeds were sown in 1914, giving about 39,000 plants, and among them again no rogue was seen.

One family however had the following history. A type plant in 1911 gave a family in 1912, about 60 plants, all types (except two doubtful, which gave only types in 1913). A typical plant in this family gave about 60 in 1913. The best grown of these, all strictly typical, were harvested *en masse*, and their seed was sown in 1914. The crop consisted of about 5100 plants of which six were rogues of an extremely low grade, being moreover *sterile*[1].

Plants of a similarly very low rogue were seen as great rarities in a crop of Gradus growing for seed in Essex. They, also, were apparently sterile. A leaf of one of them is figured on Pl. V, fig. 9, together with a leaf of the type of Gradus, and one of the ordinary rogues in the crop.

The whole course of the evidence is thus quite inconsistent with the supposition that the rogues appear as regular recessives in the ordinary sense, and we are convinced that the commercial growers are perfectly right in asserting that a strain may breed true for a while and then throw rogues. The question arises, can such rogues have been introduced by insect-fertilisation? As a very great rarity accidental cross-fertilisation does certainly take place in peas. In the course of many years' experience of peas we have met with undoubted cases at least three times. Twice we have seen a pod of yellow, round seeds on a green, wrinkled variety, and these seeds gave ordinary Mendelian results. Once in a sowing of tendrilled, white-flowered plants one heterozygous for purple and for the acacia character appeared, and this gave a normal Mendelian F_2. A few similar cases also have been given us by Messrs Sutton. These occurrences are excessively rare, happening perhaps once among many thousand plants, even when distinct varieties are grown in large numbers near each other. But in the case of the rogues it must be remembered that there is no large body of rogues from which the fertilisation could take place. They are utterly unlike any modern variety. Great efforts are

[1] See p. 251, note.

made to exterminate them, and though doubtless an occasional individual gets missed, it cannot possibly be supposed that these survivors can continually pollinate the surrounding types.

Lastly, in the particular case of Duke of Albany just described the rogues were quite peculiar, and in them the general reduction in size of the foliar parts went far beyond anything we had ever met with in our own cultivations. The leaflets were very narrow and almost strap-like, having also an abnormal neuration resembling Fig. 9 *C*, Pl. V. Nor can these rogues be supposed to have been a special F_2 form extracted from a cross with the ordinary rogues, for in the whole crop there were no other rogue-forms at all. Whether the collateral families which up till now have thrown no rogue will continue thus pure is of course uncertain.

The rogues breed true

To this statement there has been no exception in any of the three varieties (N.P.U.; D.A.; E.G.). The behaviour of the intermediates in E.G. will be described immediately, but the definite rogues whenever they appear, and however bred, are in our experience incapable of throwing any form higher, that is to say, more like the type, than themselves.

Intermediates in Duke of Albany

Typical plants of D.A., self-fertilised, with us have not thrown definite intermediates comparable with those thrown by E.G. In any row however plants with somewhat smaller parts may occur, and from a commercial sample we have even raised a strain of such plants. But in crossing type and rogue in D.A. we raised in 1914 a family ($\frac{38}{14}$) containing two plants resembling the E.G. intermediates (besides three actual rogues). The offspring of these will be seen in 1915.

The intermediates in Early Giant

Between the rogues having all the characters enumerated above and the types there are in E.G. intermediates of several kinds. These are difficult to classify, but speaking generally, we have been able to recognise besides the types and the rogues a third group which have the curved pods of the rogues combined with stipules and leaflets not markedly different from those of the types. In such plants the development of the foliar parts often, though not always, varies with their position on the stem, the lower being the most developed and nearest the type, the upper being smaller and more rogue-like. These intermediates judged in their younger stages are not distinguishable from types, and but for their curved pods might often pass un-

noticed. The point is not capable of exact proof, but we doubt whether the leaves and flowers of these intermediates are ever quite so fully developed as they are in fine typical plants.

The marbling on these plants varies in amount roughly with the extension of the parts, the most rogue-like being the least marbled.

In addition to this comparatively definite class of intermediates, plants are not uncommon, which, though in most respects typical, yet show a degree of curvature in the pods slightly greater than that of the usual type, or even occasionally a pod so much curved as to be mistakable for that of a rogue. Such plants have not been systematically counted, and the evidence showed that they cannot be regarded as genetically distinct from the types.

On the other side of the scale, among the plants which are unmistakable rogues in all other respects there are variations in the size of the parts, and occasionally one of these plants may have stipules and leaves so large as to suggest that it belongs to the intermediate class. In all these individuals however the pods are thoroughly curved.

To resume: in descending series from the type the plants may be classified thus:

1. *Types.* Leaves and stipules large and not pointed. Surface marbled. Pods straight.
2. *Types:* as above. Pods occasionally curved, or even all slightly curved.
3. *Intermediates.* Leaves and stipules nearly as in type; but usually declining, especially in upper parts of plant, towards the smaller size and shape characteristic of rogues. Pods definitely curved.
4. *Rogues.* Foliar parts (especially at lower nodes) somewhat larger than those of the ordinary rogues. Little marbling. Pods curved.
5. *Rogues.* Foliar parts small and pointed. Little or no marbling. Pods curved.

This classification is to some extent arbitrary. Owing to intergradation, and especially to the fact that the different parts of the same plant are frequently not uniform, it is not possible to refer the individuals to the several classes with perfect certainty. This applies especially to the distinctions between classes 1 and 2, and classes 4 and 5 respectively, and these minor subdivisions have not been systematically recorded.

Genetic Behaviour

The offspring of classes 4 and 5 are always rogues. As to the interrelation of these two classes it is remarkable that the great majority of the offspring of class 4 belong to class 5. Nor have we ever had a clear example of a plant which could be reckoned as belonging to class 4 coming as the offspring of class 5. On no occasion has a plant of class 4 bred true to that type, or even given more than a small proportion of plants like itself. In other words, the larger-leaved rogues throw a great majority of the ordinary small-leaved rogues, and these always breed true.

As to the genetic behaviour of the other classes the facts are not wholly clear. Difficulty of course arises from the impossibility of referring the individuals to the various classes with perfect consistency, and the genetic composition cannot be quite certainly determined from an inspection of the somatic characters. Many families contain occasional plants of class 2, namely types in general conformation, but having some slight degree of curvature in one or more pods. Plants of this sort have as a rule proved to be, genetically, types.

Classified however according to the offspring which they produce the whole series of plants (other than the rogues, which, as stated above, give nothing but rogues) can readily be divided into two main groups according as they produce

A. Families consisting of a large majority of typical plants with only occasional individuals belonging to the lower grades.

B. Families consisting of few typical plants and a majority of the lower grades.

The plants that have thrown families of the A group were:

Typical plants of class 1.
All the plants of class 2 except one.
Three plants of class 3.

The plants that threw families of the B group were:

None of class 1.
One plant which had been reckoned as class 2.
Thirteen plants of class 3.

Families of Group A

Of these there were in all 137 of which the records are sufficiently complete, and of them 77 families, aggregating about 3800 plants[1],

[1] In some families recorded as true before the general course of the phenomena was known we have only estimates of the totals, and hence the precise numbers cannot be given.

contain nothing lower than class 2. These we regard as breeding true to type. The remaining 60 families contained the lower or aberrant plants with greater or less frequency.

Of these 60 families 42 were from parents in every way typical and the immediate offspring of types. They gave

2154 of classes 1 and 2,
48 of class 3,
31 of classes 4 and 5,

or 2154 types to 79 aberrants, viz. 27·3 : 1.

4 families were from parents in every way typical but extracted from class 3 parents. They gave

243 of classes 1 and 2,
4 of class 3,
3 of classes 4 and 5,

or 243 types to 7 aberrants, viz. 34·7 : 1.

11 families were from parents reckoned as class 2. They gave

634 of classes 1 and 2,
17 of class 3,
13 of classes 4 and 5,

or 634 types to 30 aberrants, viz. 21·1 : 1.

The remaining 3 families contained a distinctly higher proportion of aberrants, though these were still a small minority. They gave

162 of classes 1 and 2,
16 of class 3,
9 of classes 4 and 5,

or 162 types to 25 aberrants, viz. 6·5 : 1.

It is likely that these three form a distinct genetic group, and the parents of all three were classified *as belonging to class* 3, which combine the foliar structures of the types with the curved pods of the rogues.

The details of these three families were as follows:

Reg. number	Classes 1 and 2	Class 3	Classes 4 and 5	Ratio
1914				
122	33	0	4	8·25 : 1
137	50	6	1	7·1 : 1
145	79	10	4	5·6 : 1

The details of the other families cannot as yet be regarded as important, nor can any significance be attached to the particular composition of the first 57 families at all events. Since the frequency of the aberrant plants is so small it is evident that many of the families included among the 77 which contained no aberrants may have been capable of producing them. All that can be positively declared is that individuals, thoroughly typical, are capable of throwing the lower forms sporadically in small numbers, and that the genetic behaviour of classes 1 and 2 is approximately the same.

Families of Group B

There are 16 families of this kind, namely containing a minority of types and a large majority of aberrants. The proportions seem altogether irregular, and they range from 1 type : 64 aberrants (No. *118) to 1 type : 2 aberrants (No. 112).* Of the 16 parents 15 were of class 3 and 1 was of class 2.

The details are as follows:

Parent	Reg. number	Offspring: Classes 1 and 2	Class 3	Classes 4 and 5
	1913			
Class 3	92	6	8	64
„	113[1]	0	4	81
„	117	5	7	89
„	118	1	2	62
	1914			
„	116	6	4	28
„	117	15	8	63
„	127	7	11	19
„	128	3	3	81
„	147	4	61	57
„	148	2	0	37
„	160	6	32	21
„	161	2	10	10
„	162	2	8	23
„	173	2	0	21
„	112	45	8	85
Class 2	*155*	*10*	*15*	*13*

These 16 families give a total of 116 typical and 935 aberrant, but it is obvious that there is no uniformity in their composition. The last

[1] Though this plant gave no offspring typical it may be included here, because the family is obviously of the same general composition as the rest, and because the *families 160–2 descend from it.*

two differ considerably from the rest in containing a distinctly higher proportion of typical plants. The parent of one of these was moreover classed as class 2.

The genetic behaviour of the types and intermediates may now be summarised as follows:

Perfectly typical plants often breed true, but they may throw any of the aberrant forms, though never more than a small percentage of them.

Plants of class 2 commonly behave genetically like the types themselves. We have included in class 2 such plants as have straight pods together with others showing some curvature, but most of this class consists of plants with a low degree of curvature in many pods (as Pl. VII, fig. 15). Those which had any straight pods at all behaved genetically like types. One plant (155) however which had only a slight degree of curvature was proved by its offspring to be of the genetic composition of class 3. Three plants genetically of Group A, were shown by their offspring to differ in composition from most of that Group, inasmuch as they threw a higher proportion of aberrants, and it is noticeable that these three plants (122, 137, 145) had on their somatic structure been reckoned as class 3.

Most of class 3, the real intermediates, must be genetically quite different from the types of classes 1 or 2, for instead of throwing a large majority of types, they give a large majority of rogues.

From what has been said it will be observed that plants with curved pods can throw some plants with straight pods, but plants with rogue foliage cannot throw offspring with typical foliage.

As regards the correctness of our discriminations of the classes when tested by genetic results, it will be observed that in addition to the plant referred to class 2 which behaved like class 3, there were also the three plants assigned to class 3 which behaved like low members of Group A. Judgments therefore based on somatic appearances give in this case a rough, but by no means accurate, indication of genetic behaviour.

Allowing however for some error in the classification of the families, the proportions in which the aberrant forms are produced by the types are such as to make it extremely unlikely that they are expressions of any ordinary factorial system. It might for example be supposed that the type leaves or the straight pods were each dependent on the presence of one or more factors. Any scheme based on the hypothesis that these factors are distributed in any of the

ordinary ways must however fail, not merely on account of the rarity of the aberrant individuals of the various classes collectively, but on account of the numerical relations of the aberrant classes to each other. On the other hand an equally unconformable phenomenon appears in the circumstance that the plants of class 3 are able to *produce thoroughly typical offspring which breed as true as the types.* We have then to reckon with the paradox that the types, without crossing, can occasionally produce the intermediates, and that these, in their turn, can, also by self-pollination, produce types.

From the fact that the rogues never threw any of the higher classes we at first were inclined to regard them as recessives and class 3 plants as heterozygotes, leaving the question of the number of factors involved in abeyance. Since class 3 never breeds true and throws both types and rogues, each of which behaves genetically like the other members of those classes, the suggestion that class 3 is heterozygous seems at first sight plausible; but here again the numerical composition of these families makes any such supposition quite inapplicable.

The interrelations of classes 4 and 5 are equally obscure. Inasmuch as class 4 never breeds true, it cannot be regarded as homozygous in the usual sense; nor in view of the fact that it throws almost exclusively plants of class 5, can it be represented in any simple way as heterozygous.

Crosses between Types and Rogues

We have next to consider the remarkable evidence provided by the crosses. *It relates in the first place to 52 families raised* by *crossing* thoroughly typical plants with rogues of classes 4 or 5. Of these cross-bred families 50, containing 284 plants, *when fully grown,* were thorough rogues in all respects, none reaching a development higher than that of class 4, most of them being class 5. As shown in the Table these crosses were made not only in Early Giant and in Duke of Albany but also in Ne Plus Ultra. We have in addition 4 families raised by crossing E.G. with a rogue from a dwarf variety and 2 from N.P.U. fertilised from a rogue in "Exhibition."

In some the type was used as mother and in others as father, but the results were the same.

Fourteen of these plants which we may call F_1 were bred from and gave 949 plants all rogues, none of which reached a development higher than that of class 5. The F_3 plants were also rogues without exception. This evidence taken together with the fact that no rogue,

however produced, has given anything but rogues, may be taken as proving conclusively that the elements, whatever they may be, which cause the distinction between the type and the rogue, are absent altogether from the rogue. The types can produce both intermediates and rogues; the intermediates produce a few types and many rogues, and the rogues breed true[1].

CROSSES

1. *Type* ♀ × *Rogue* ♂

Reg. *number*	*Female*	*Male*	Offspring: Number	Offspring: Juvenile condition	Offspring: Adult condition
1912					
88	D.A. type	D.A. rogue	9	—	rogues
89	,,	,,	9	—	,,
90	E.G. type	E.G. rogue	2	—	,,
91	,,	,,	9	—	,,
94	N.P.U. type	N.P.U. rogue	7	—	,,
95	,,	,,	4	—	,,
1913					
337	,,	rogue in "Exhibition"	5	—	,,
338	,,	,,	2	—	,,
1914					
2	E.G. type	E.G. rogue	6	—	,,
3	,,	,,	6	2 ? type	,,
4	,, (class 2)	,,	7	1 ? type	,,
5	,, type	,,	7	5 v. near type	,,
6	,,	,,	6	near type	,,
7	,,	,,	9	,,	,,
8	,,	,,	9	,,	,,
9	,,	,,	1	rogue	,,
10	,,	,,	1	,,	,,
12	,,	,,	4	3 ? type	,,
29	,,	,,	9	near type	,, (2 class 4)
30	,,	,,	1	,,	,,
31	,,	Dwarf rogue	8	7 near type	,,
33	,,	D.A. rogue	8	near type	,,
34	D.A. type	E.G. rogue	8	,,	,, (1 class 4)
57	E.G. type	,,	7	,,	,,
63	,,	,, (class 4)	10	,,	,,
64	,,	,, ,,	7	,,	,,
67	,,	,, ,,	9	,,	,,

[1] As it was conceivable that this behaviour of the rogues was due to apogamy, experiments were made to determine whether this phenomenon occurs. No indication of a positive result was however obtained, nor have we ever seen seed formed in the course of many similar trials made in the past with various forms of *Pisum*.

2. Rogue ♀ × Type ♂

Reg. number	Female	Male	Offspring: Number	Offspring: Juvenile condition	Offspring: Adult condition
1912					
92	E.G. rogue	E.G. type	2	—	Rogues (some steriles in F_2, see text)
93	,,	,,	1	—	
1914					
13	,,	,,	6	1 near type	rogues
14	,,	,,	5	3 near type	,,
15	,,	,,	4	type	,,
16	,,	,,	3	,,	,,
17	,,	,,	4	near type	,,
18	,,	,,	2	,,	,, (1 class 4)
20	,,	,,	5	type	,,
21	,,	,,	7	near type	,, (1 class 4)
22	,,	Dwarf type	9	type	,, (class 4)
23	,,	,,	4	,,	,, (1 class 4)
24	,,	,,	1	near type	,, ,,
25	,,	E.G. type	6	5 near type	,,
32	Dwarf rogue	,,	1	near type	,,
37	D.A. rogue	D.A. type	9	,,	,,
38	,,	,,	5	,,	3 rogues, 2 intermed.
39	,,	E.G. type	6	5 near type	rogues
40	,,	,,	5	type	,, (1 class 4)
43	,,	D.A. type	3	,,	,, ,,
44	,,	,,	8	rogues	,,
45	,,	,,	7	near type	,, (1 class 4)
53	,,	,,	9	,,	,,
70	E.G. rogue (class 4)	E.G. type	3	1 near type	,,
71	,,	,,	5	near type	,,

Crosses between Type and Intermediate (Class 3)

Reg. number	Female	Male	Offspring: Number	Offspring: Juvenile condition	Offspring: Adult condition
1914					
49	D.A. type	E.G. class 3	1	near type	rogue[1]
50	,,	,,	8	,,	5 intermed., 3 rogues
69	E.G. class 3	E.G. type	7	,,	4 type, 3 intermed.
68	,,	E.G. rogue	6	rogues	rogues

[1] See final note.

Crosses between Rogues and Rogues

Reg. number	Female	Male	Offspring: Number	Offspring: *Juvenile* condition	Offspring: *Adult* condition
1914					
51	D.A. rogue	D.A. rogue	9	rogues	rogues
54	,,	E.G. rogue	3	,,	,,
55	,,	,,	6	,,	,,
56	,,	D.A. rogue	8	,,	,,
59	E.G. rogue	E.G. rogue	7	,,	,,
60	E.G. rogue, class 4	,,	7	,,	,,
61	E.G. rogue	,,	7	,,	,,
62	,,	,,	8	,,	,,
65	,,	E.G. rogue, class 4	4	,,	,,
66	,,	,,	5	,,	,,

We have stated that the so-called F_1 plants, when adult, were thorough rogues. *In the juvenile condition* however the majority of them, judged by the size and shape of leaves and stipules, differed little if at all from the types. Actual rogues of classes 4 and 5 can be distinguished from types as soon as any leaves appear. By the time the sixth or seventh leaf is unfolded the difference is clear even to the inexperienced. In the case of most rogues bred in F_1 the lower leaves and stipules in size, shape, and marbling are almost if not quite like those of the types, and until about the 8th node is reached we cannot as a rule distinguish them. After that level the narrowing of the parts begins, and the rogue characteristics are rapidly assumed (cp. Pl. IV, figs. 6 and 7). In some of the families the course of development was not noted, but of 41 families which were more carefully watched most of the members of 34 families are recorded as beginning like types and *three families only (10 plants) as beginning in the rogue-like condition.*

It might be supposed that the more luxuriant growth of the F_1 seedlings was, as it so often is, an incidental result of crossing; but this suggestion is negatived by the experience of 10 crosses made *between rogues*, giving 64 plants which were characteristic rogues from the first, without any symptoms of extra luxuriance.

Besides the 50 families raised from rogue × type or reciprocal which behaved in the way described, there were two exceptional cases[1].

[1] In $\frac{92}{12}$ F_1 from E.G. rogue × E.G. type was a rogue as usual, but among 19 F_2 plants derived from it were 4 steriles. The flowers did not open properly and the pollen was deficient in amount. One artificial pollination failed. Probably this sterility was a recessive condition, but whether it affected one sex or both was not clearly made

1st Exception. In this ($\frac{92}{12}$) an E.G. rogue fertilised by a true type gave 2 seeds of which one grew to be adult. This F_1 plant was recorded as having *leaves like type*, but curved pods. Judging from the offspring *it produced, this plant was probably of the kind which we came* subsequently to recognise as class 2, namely type-plants with some degree of pod-curvature, behaving genetically as types. In F_2 it gave a family of 38 plants. They were not very well grown, but their characters were in all respects those of *types*, several having pods slightly curved, but none in any way approaching rogues. Two of these gave moreover offspring in F_3, 21 and 57 plants respectively, all well grown plants in all respects typical, occasional pods being slightly curved, as may happen in any family of types.

There is in this case complete certainty that the original *mother* was a rogue, for the normal offspring of that plant have been grown for three generations. All are thorough rogues, and the strain has been used repeatedly for crossing, giving the results which we have come to look on as normal.

Seed of the original father was unfortunately not kept.

2nd Exception. In this ($\frac{38}{14}$) a cross of D.A. rogue × D.A. type gave 5 plants, of which 3 were rogues *and* 2 *were intermediate*, being the only D.A. plants we have bred which look comparable with the definite intermediates so often bred in E.G. Their offspring will be seen in 1915.

We have no interpretation of these remarkable exceptions as yet to offer.

Crosses with Intermediates

Since crosses between rogues and types give rogues only (with the two exceptions named), it was to be expected that crosses between rogues and intermediates would do the same. This cross was made only once and gave six rogues ($\frac{68}{14}$).

More interest attaches to the crosses between the intermediates (class 3) and the type. The result of this mating is known in three cases only (see Table, 49, 50, 69). It will be observed that in one case

out. The seed of the parents used in the original cross was not preserved and it cannot be said if sterility existed as a recessive on either side of the parentage. Recessive sterility is of course not uncommon among plants, especially in connection with the male side. As already stated, we had on one occasion sterile rogues in D.A. It is interesting to notice also that from Andrew Knight's description of his experiments in crossing peas he clearly had a strain affected with male sterility, which phenomenon, in accordance with the scientific ideas of those days, he attributes to prolonged cultivation in one locality (*Phil. Trans.* 1799, p. 196).

the type E.G. was the father, and in the other two the type D.A. was used as mother. The evidence is meagre, but it supplies proof of the important fact that neither sex of the class 3 intermediates can be *homogeneous*.

Discussion

The general course of the phenomena is evidently quite unlike anything with which we are familiar in ordinary Mendelian inheritance. Since the types can throw rogues and the rogues cannot throw types, it seems clear that the types contain something which the rogues do not contain. This something however is different from an ordinary Mendelian factor both in the effects of its presence and in the manner of its distribution among the gametes.

As stated in the introduction the visible differences (apart, that is, from the difference in flavour of the seeds) between type and rogue are essentially quantitative. The distinctions affect the shapes of the organs, but possibly all of them, even the striking difference between straight and curved pods, may be consequences of greater or less extension, and we incline to think that the rogue is really a form wanting in some particular kind of luxuriance or power of amplification. The difference is of course not merely one of size, for rogues may be large and types may be small; but it must be rather some quality of extension, dependent on cell-division occurring chiefly at right angles to the axis of growth.

Since the curved pods may be combined with foliar parts approximately like those of the types, it seemed at first sight possible that these two characters might be governed by separate factors of the familiar kind, but the genetic evidence at once disproves this suggestion. The composition of the families in which rogues appear from types makes any scheme of this kind inapplicable, and the fact that the families derived from intermediates consist chiefly of rogues is of course quite at variance with such a possibility.

As regards the appearance of rogues from types we plainly have to deal with an irregular phenomenon. The gametes capable of producing rogues are given off sporadically and not in accordance with any system that we can perceive. This is abundantly proved by much evidence and especially by the case of the strain of Duke of Albany quoted at the beginning of this paper, in which a strain after breeding true on a large scale for two generations gave rise to six thorough rogues. In view of this irregularity it may be supposed that some

ıenomenon of *mosaicism* may be *involved*. We have much *inclined* this hypothesis. Can the type-plants or some of them contain ıslands" of rogue tissue? When characters are distributed in a .ant mosaically, that is, to speak strictly, *not according to any ometrical system*, families of irregular composition are to be expected. he formation of *rogue-gametes* by the types must be describable in ıese terms, but we can get no evidence that the somatic tissue of the pes is thus actually mosaic. We have often sowed seeds from the ıost curved pods on plants otherwise type, but rogues did not come ith increased frequency from such pods. In one case a whole branch ad curved pods while another branch was typical, but all the offspring ere typical. The evidence suggests that there is a gradation in enetic proportion from the types which breed approximately true to ıe intermediates which throw a large majority of rogues, the group f three plants which gave only 6·5 types to one rogue forming a onnecting link between them. Moreover the fact that these three lants were reckoned as of the intermediate class when judged by heir somatic characters, proves that the somatic gradation imperectly corresponds with the genetic. But there is still a wide gap etween 5·6 types to one rogue as found in family 145 (p. 245) and ne type to two rogues as found in family 112 (p. 246).

No hypothesis of mosaicism, even if otherwise probable, will repreent the results of crossing types with rogues, which are, so far as we now, without any close parallel among plants or animals. We must uppose that the gametes concerned in the production of the crossred plants *are those which would take part in self-fertilisation*, and that ve are not concerned with any phenomenon of selective fertilisation. The results of the crosses must therefore be in reality heterozygous ınd must receive from the one type-parent those elements which if hey were united with a similarly constituted gamete of the other sex would form a type-plant. Nevertheless such plants are rogues and oreed rogues only. Therefore the type-elements received by the F_1 from the type-parent must be permanently lost. Whither do they disappear? *The only answer to this question which we can offer is that when introduced from one side only of the parentage these elements are in some way used up and cut out of the germ-lineage in the early stages of the somatic development.* The young stages of the F_1 plants are, almost always, type-like, but the characters of the type are left behind with further development.

We have also evidence that a similar change takes place in the life-

history of some at least (probably most) of the rogues which come as the immediate offspring of types. Several times families afterwards found to contain rogues, though individually examined in the early stages, were then recorded as free from rogues; and occasionally in these families plants which developed into ordinary rogues are recorded in the juvenile condition as doubtful. Rogues, offspring of rogues, never pass through such a stage. There is therefore no reasonable doubt that the rogues arising as the offspring of types are at all events frequently heterozygotes formed by the union of type and rogue gametes, and since they always breed true, in them also the type-elements must be lost in some somatic stage.

Some light may perhaps be obtained by examining the produce of seeds from the various parts of the plant separately and this we shall endeavour to do, but it is likely that by the flowering stage the differentiation, or segregation if the term be applicable, has already been effected. Nevertheless in plants of the intermediate class the apical parts are so much more rogue-like than the rest that the experiment ought to be made.

We incline to think these indications point to some process of somatic segregation which prevents the type-elements from reaching the germ cells of the cross-bred plant. A comparison may perhaps be suggested between this phenomenon and the examples, fairly frequent in horticultural literature, of plants which produce from root-cuttings forms different from those arising by the propagation of shoots or buds above the root-system.

It may be mentioned that the genetic behaviour of the ordinary factors introduced in crosses with rogues is normal. For example the rogue F_1 from D.A. × E.G. bears the usual yellow and green seeds. One of our D.A. strains throws albino seedlings which die. Such albinos appear as normal recessives among the offspring of F_1 rogues raised from crosses with that strain, and other similar instances have occurred. Clearly therefore there is no general exclusion of the contribution of the type-parent, and it is only the features special to the type which are excluded.

The nature of the difference between Type and Rogue

The genetic behaviour is, as we have said, without parallel, and even for the differences themselves there is no very plain analogy. The most obvious is that distinguishing giant forms from those of ordinary size in several plants, especially in *Primula*. Provisional

counts of the chromosomes in the peas have not shown numerical differences, but our experience of such work is small and pending an expert report which we are obtaining, the matter must be regarded as doubtful. In *Primula sinensis* however Gregory has described a giant race differing greatly in size from the ordinary type though the chromosomes were not more numerous. But in no case, so far as we know, in which giant forms have been observed, do these throw offspring in any way comparable with our rogues. Nothing of the kind is recorded for *Primula kewensis*, *Œnothera gigas*, or either of the giant forms of *Primula sinensis*. In genetic behaviour all these cases differ entirely from ours.

In this connection perhaps the case of tulip "thieves" may be mentioned. These plants arise from ordinary, broad-petalled tulips, and are distinguished by their narrow, pointed petals[1]. As to their genetic properties we have no information, but the differences between them and the type from which they come is somewhat suggestive of those with which we have dealt.

Messrs Sutton have called our attention to somewhat similar rogues with *erect* pods thrown by Broad Beans (*Vicia faba*) with drooping pods. We have begun to investigate this case, but we incline to suspect that these rogues are in reality derived from crosses with the variety known as the Horse Bean, in which the pods are erect.

Historical Evidence

Messrs Sutton have most kindly made a search of their trial-records back to 1886 in the hope of discovering something as to the frequency of rogues in the history of well-known varieties. There are continuous records of the following:

American Wonder, Blue Peter, British Queen, Champion of England, Daniel O'Rourke, Dr McLean, Duke of Albany, Earliest Blue, Eclipse, Fillbasket, McLean's Little Gem, Ne Plus Ultra, Pride of the Market, Prince of Wales, Sangster's, Telegraph, Telephone, Triumph, Veitch's Perfection, Walker's Perpetual, Yorkshire Gem, Yorkshire Hero. The trial sample in each case consists of 200–300 seeds. Of the varieties named, the following six have produced rogues with especial frequency: Dr McLean, Duke of Albany, Ne Plus Ultra, Pride of the Market, Telegraph, Telephone. Plants not true to type of course may come occasionally in any variety, but the "wild"

[1] Solms-Laubach, *Weizen und Tulpe*, Leipzig, 1899, p. 71; and Krelage, *Gard. Chron.* 1881, II, p. 182.

rogues with which we are concerned are only rarely recorded as appearing in the other 16 varieties. It is perhaps worth noting that all the six are varieties characterised by the great width of the leaves and stipules. On the other hand Fillbasket, of which Denaiffe remarks "feuillage...particulièrement léger pour une race demi naine," is not once recorded to have thrown one of these rogues.

Certain varieties have pods curved as a normal feature, and, since they have already one of the definite rogue features, it might be expected that they would commonly throw rogues. It is noticeable however that, according to several trials recorded by Messrs Sutton, the variety Gladstone threw no rogues in our sense, though this variety has pods markedly curved. Of other curved types we have no evidence.

From the indications given we incline to think that the production of rogues is a consequence of some instability connected with great lateral extension of the parts.

From the genetic evidence[1] it is clear that in order to influence tbe somatic structure beyond the juvenile stage, or to appear in the germ cells, the character, whatever it is, must be introduced from both sides of the parentage.

In the business of harvesting we have had the benefit of much assistance from many workers at this Institution, to whom our thanks are due. During 1914 also, Miss Ida Sutton, one of our Minor Students, took part in recording and generally in the experimental work.

[*Note added June*, 1915. The paper gives results to end of 1914. The work of 1915 has added one point of considerable importance. The cross-bred plant 49 of 1914 (p. 250), booked as rogue, had a branch somewhat type-like in character, the next being thoroughly rogue. Seed saved from the rogue parts have given all rogues, but the seed of the type-like branch has given some type-like plants in addition to many rogues. Details will be given in a later communication. The case is of considerable significance as adding not only another exception to the general behaviour of the crosses, but also actual proof that a plant can be a true mosaic of rogue and type.]

[1] The exceptions must be remembered.

EXPLANATION OF PLATES

PLATE II

Fig. 1. Stipules and leaf of type (Early Giant).

Fig. 2. Another leaf of Early Giant.

Fig. 3. Comparable stipules and leaf of Early Giant rogue.

These three figures are from plants grown in pots indoors. They were drawn by Mr Osterstock.

PLATE III

Fig. 4. Stipules and leaf (right hand) at 10th node of Duke of Albany. Stipules and leaf (left hand) at top of stem.

Fig. 5. Stipules and leaf of Duke of Albany rogue. Left-hand figure from 14th node. Right-hand figure from top of stem.

PLATE IV

Fig. 6. *A*. Stipule and leaf from 6th node of a young seedling Early Giant type. *B*. The same from the 7th node of the same plant, showing shape of the apex of leaf when folded. *C*. The same parts from a seedling Early Giant rogue. *D*. The same from the 7th node of the same plant, showing shape of the apex of the leaf when folded.

Note that in *B*, the type, the apex of the leaf is cut square, whereas in *D*, the rogue, it is pointed.

Fig. 7. Stipules and leaflets of F_1 seedlings (type × rogue). *A*. Stipule of 6th node. *B*. Leaflet of 6th node. *C*. Leaflet of 7th node before unfolding. *D* and *E*. Stipule and leaflet of 5th node. Note resemblance of these parts to those of type plants.

PLATE V

Fig. 8. Rogue resulting from the cross type × rogue in Early Giant. *A*. Stipule and leaf of 9th node. *B*. Stipule and leaf of 20th node.

Fig. 9. *A*. Leaf of Early Giant type. *B*. Leaf of Early Giant rogue. *C*. Leaf of sterile rogue found in Gradus (p. 241).

All these three are taken from above the middle of the stem.

PLATE VI

Fig. 10. Whole plant of Early Giant rogue, class 5.

Fig. 11. Whole plant of Early Giant rogue, class 4.

Fig. 12. Whole plant, Intermediate, class 3, with foliage much as in the type, even to the top of the stem, but *pods curved* as in rogue.

Fig. 13. Early Giant type. At top of lateral stem is one curved pod (see p. 242).

PLATE VII

Fig. 14. Pods. *A*. Straight as in Early Giant type. *B*. Curved, as in Intermediate, class 3. *C*. Curved and narrow, as in rogue.

Fig. 15. All the pods of a plant of Early Giant which bore both straight and curved pods. Chosen as an extreme case of approach to class 3; but like other such plants bearing this mixture of pods it was proved by its offspring (20 typical) to be genetically a type of class 2.

Fig. 2.

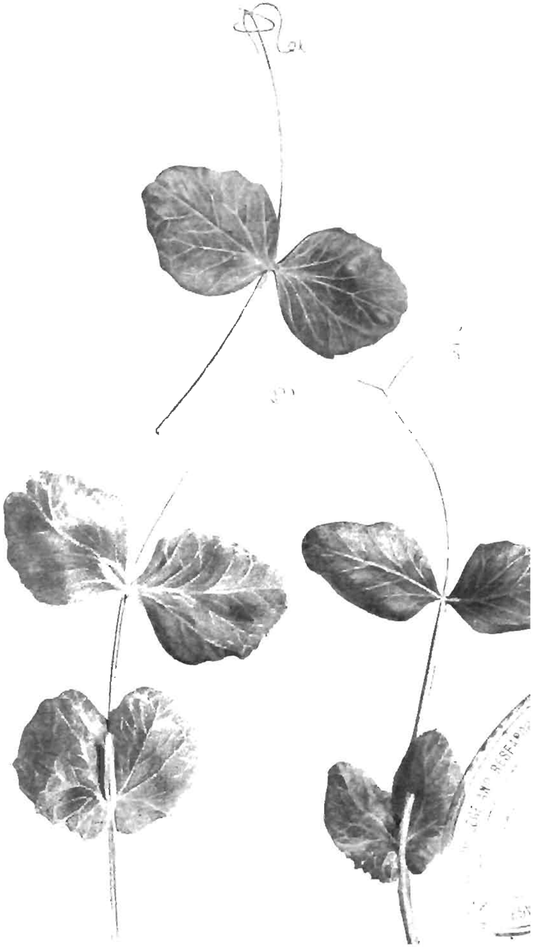
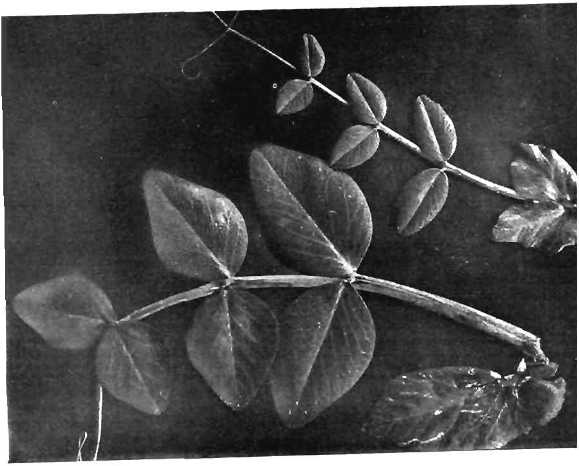
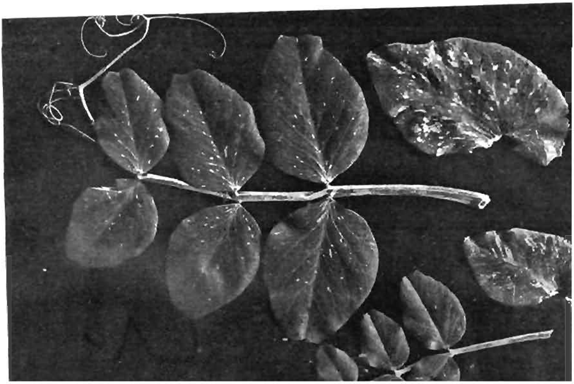


PLATE III





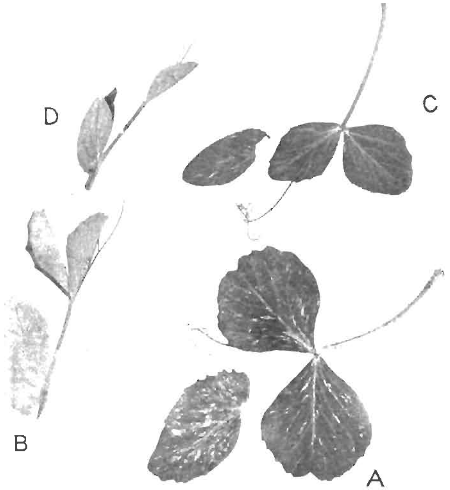


Fig. 6.

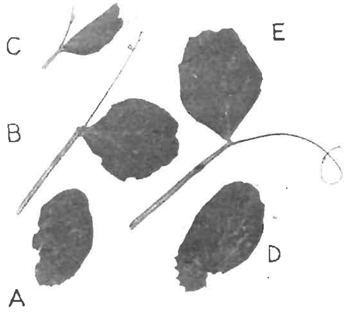


PLATE V

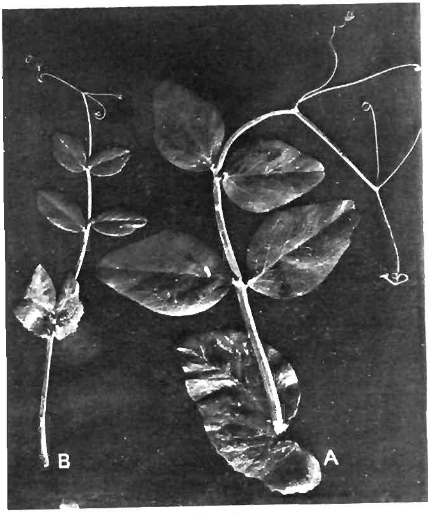


Fig. 8.

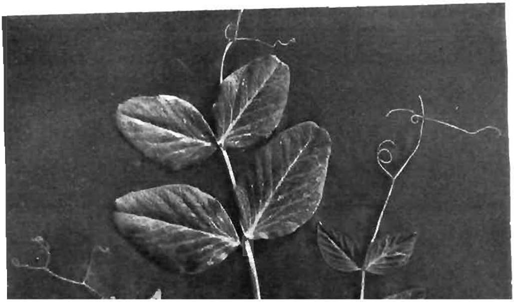


PLATE VI

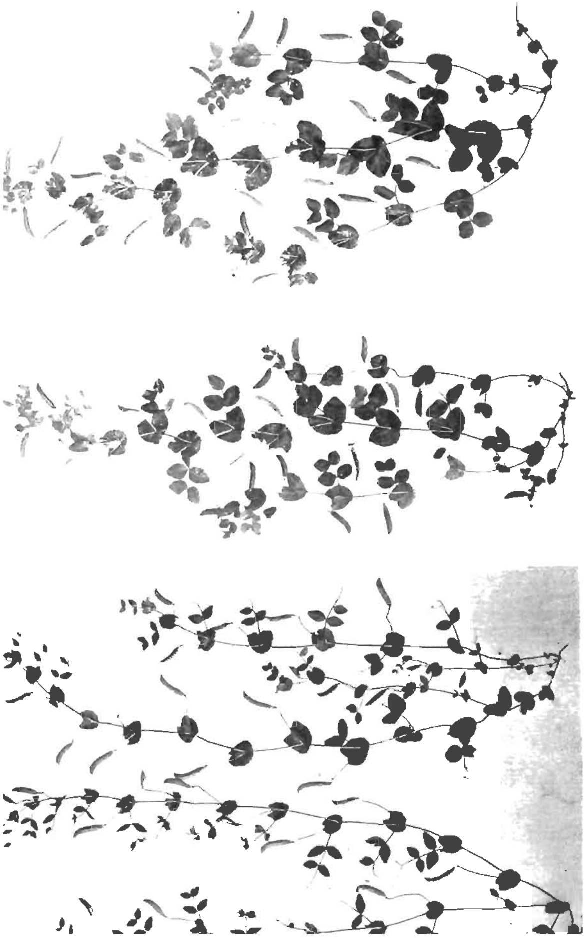


Fig. 14.

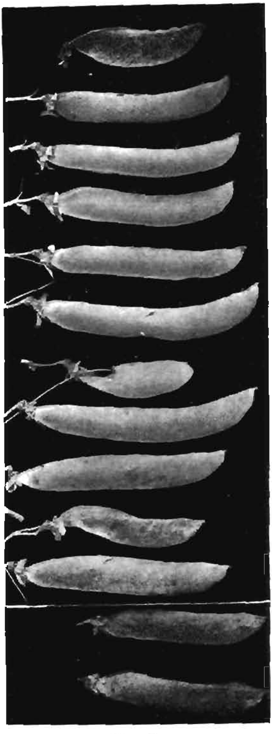


Fig. 15.

NOTE ON AN ORDERLY DISSIMILARITY IN INHERITANCE FROM DIFFERENT PARTS OF A PLANT

[*Proceedings of the Royal Society*, B, LXXXIX, 1915]

IN a recent paper[1] we described the genetic behaviour of the peculiar, wild-looking, "rogue" peas which appear as the offspring of the cultivated types. In several respects the phenomena are as yet without parallel. The genetic constitution of the F_1 plants raised by crossing types with rogues was especially remarkable. These plants, as young seedlings, are intermediate between types and rogues, but, with rare exceptions, as they mature they become normal rogues and behave genetically exactly like pure-bred rogues, producing only rogues as offspring. We conjectured that a segregation of factors takes place in the soma, such that the type elements are left behind in the base of the F_1 plant and are thus excluded from the germ lineage.

The observations here described, though very imperfect, are entirely consistent with the facts related above and with the interpretation offered. As a season must elapse before the evidence can be materially increased, we venture to make this preliminary record.

In the paper referred to we described certain intermediate forms found in Sutton's "Early Giant" (a strain of Gradus). The offspring of these plants shows them to be commonly of two classes: those which throw predominantly rogues and some types, and those which throw predominantly types and a few rogues. The characters of such intermediate plants often change progressively with growth in the direction of the rogue form, the lower parts being more type-like, the upper parts more rogue-like. This fact, taken together with the observation that it is only the lowest leaves of the F_1 plants which show any influence of the type-parent, suggested that when the offspring consists of a mixture of types and rogues, the types may be derived from the lower pods and the rogues from the upper pods. To test this possibility we this year saved the upper and lower pods separately from many plants. The bulk will be sown next spring, but, though the results of autumn sowing are unsatisfactory inasmuch as the plants cannot reach maturity, we have made a preliminary trial with a small quantity of seed. Three families came up which contain

[1] *Journ. Gen.* v, 1915, p. 13. [This volume, p. 236.]

the requisite mixture of forms. Several plants were unfortunately damaged by Noctuid larvæ and had to be reckoned as doubtful, but the general result of the experiment is quite clear.

	Types	Dubious	Rogues
Family 1			
Pods at 9th to 11th nodes	2	9	3
Pods at 12th to 15th nodes	—	—	23
Family 2			
Main stem—			
9th to 14th nodes	2	5	5
16th to 18th nodes	—	3	7
Branch from 2nd node—			
6th to 9th nodes	3	14	—
10th to 12th nodes	—	—	12

From these six sowings it is evident that the two parents were of the kind which throw a majority of plants lower, that is more rogue-like than the type, together with a few typical plants which were the produce of the lower pods. This was the case both in the main stem and in a branch from the base.

In the third family we had from the 9th to 13th nodes 15 types, and 11 which were almost certainly types, though not well characterised, while from 14th to 17th nodes we had 2 types, 5 below type, and 4 which were almost certainly true rogues. The parent of this family was therefore of the class which throws a large majority of types and a minority of lower forms, and again the lower forms were among the produce of the upper pods.

We have therefore little hesitation in saying that in these plants a segregation takes place in the soma of the plant, such that the type elements are present especially in the lower parts, just as had been surmised from the structure of the F_1 generation.

In view of this evidence it is probable that rogues which arise directly from typical plants are derived predominantly from the apical pods. Material for testing this suggestion will be sown next spring.

NOTE ON EXPERIMENTS WITH FLAX AT THE JOHN INNES HORTICULTURAL INSTITUTION

[*Journal of Genetics*, v, 1916]

In connection with Dr Eyre's paper[1] the following note of our experience with flax may be of interest. In 1911 Mrs Ryan of Fort William suggested to me that an improved strain of flax might be of value to the agriculture of Ireland and of the Scottish Highlands. As I had long intended to make experiments on heterostyly in flax I obtained some samples of seed. My interest in the subject was especially concerned with the possibility of crossing the homostyled *L. usitatissimum* with some heterostyled species such as *perenne*. Except in the style-structure and habit (*usitatissimum* being strictly annual) there is no noticeable distinction between the two species. Nevertheless all attempts to cross them, however made, have failed with us. In this respect there is nothing more to report. I may mention that I used the method of emasculation described by Dr Eyre, namely bodily removal of corolla with adherent anthers, very successfully in the case of the *short-styled perenne*, but did not find it applicable to any other forms.

Many samples of seed of *usitatissimum* were kindly sent by Messrs Vilmorin. I also received others (through Dr Hinchcliff of the Department of Agriculture for Ireland) from Mr Ghekiere and from Mr de Zeeuw. Among the Irish samples was one that was said to have been saved for length of stem.

The plants in each sample were irregular in height, being obviously a mixture of several types. In most samples a few very tall plants occurred, reaching to about 4 feet, whereas the majority were about 3 feet high. I covered the flowers of one such tall plant in the sample sent by Vilmorin as "Courtrai," and fearing that there might be self-sterility I also put into one bag the heads of two such plants which were growing close together. The event showed that flax is perfectly self-fertile. The seeds of the three tall plants gave in 1912 rows of plants most of which were of the 4 foot class. Many plants of course did not reach this height and there were several small plants, but I have little doubt that the smaller plants were merely prevented from reaching their full development by crowding. The subject

[1] [*Journal of Genetics*, v, 1916, p. 189.]

seemed to be unsuitable for accurate investigation without very elaborate precautions to ensure uniformity of conditions and it was treated simply as a matter of economic interest. The height reached varies greatly with the nature of the soil and the spacing. In 1913 the seeds from the tall strain (bagged) gave plants averaging 4 ft. 6 in. with individuals 5 feet high, but this increase was obviously due to the ground chosen having suited them better; for the 1914 crop, similarly raised from them, was grown on inferior land and for the most part did not fully reach 4 feet. The 1915 crop, similarly raised from these, put on the land used in 1911 gave a very level crop 4 feet high.

The seed from the plants of 1914 which were *not* covered was collected in mass and sent to Mr F. K. Jackson, of the Leeds University Flax Experiment Station at Selby. In his Report for 1915 he says that after rain came at the end of June this flax "began to grow vigorously, and in a fortnight had outstripped all other varieties in the field, so that by harvest it was from 9 to 12 inches taller and much superior in quality." The weight of crop with the seed on was reckoned at 1 ton 13 cwt., that of the next best flax on the same land being 1 ton 8 cwt. 1 qr.

Evidently many points of genetic importance could be studied in this case by accurate methods. In 1915 Miss M. R. Michell began such work here, making crosses between plants of various heights, etc. Meanwhile it is to be noted that, as the result of our experience, the raising of a tall strain of flax is a very easy matter, and can be done by simple selection of materials already existing in common crops. I may add that at Selby in an ordinary crop growing on agricultural land I saw several individual plants clearly belonging to the tall strain, reaching about 4 feet.

To what extent crossing takes place under natural conditions I cannot say. Most seed presumably is the result of self-fertilisation. I saved seed from a white-flowered variety not covered, growing between rows of blue flax, and all the plants except one came white. (There was *some* reason also for suspecting that even this one was a stray from the next row; for the plant agreed with that row, which was of a peculiar type.) As white is recessive to blue in flax, these plants were probably from self-fertilised seed. In another case a curious dwarf form with dark blue flowers, about 1 ft. 10 in. high, was similarly tested. It had appeared originally as a single plant among crimson *L. grandiflorum*. Presumably this came from a stray

seed. In general appearance this type somewhat resembled the oil flaxes of India. A quantity of seed of this variety, gathered from uncovered plants growing beside the other flaxes, came perfectly true to type. It is therefore to be presumed that the *usitatissimum* varieties are habitually self-fertilising, at least in England. On the other hand I cannot explain the fact that the seed sent from Ireland as saved for tallness did not give a crop in any way remarkable for height.

How many genetically distinct heights exist cannot be said. Besides the oil flaxes which are about 1 ft. 9 in. high we have had certainly three heights: (1) our own tall strain, about 4 feet; (2) several ordinary blue and also white forms, about 3 feet; (3) a dark blue, true-breeding type, about 2 ft. 6 in. Each of these is genetically pure, almost beyond question, and the rows of the several types standing side by side were each in general appearance strikingly level and uniform at their respective heights.

ROOT-CUTTINGS, CHIMÆRAS AND "SPORTS"

(With Plate VIII)

[*Journal of Genetics*, VI, 1916]

SINCE the work of Baur and Winkler the extraordinary interest of plant-"chimæras" has been universally recognised. In Winkler's examples various combinations of *Solanum lycopersicum* (Tomato) and *S. nigrum* were made by grafting, and "graft hybrids" were thus produced, having one or more cell layers of the one species superposed over a core of the other species. From his studies of variegated plants Baur successfully interpreted these cases. There are many sorts of variegation, but in the commonest a "skin," one or more cell layers thick, devoid of green chloroplasts and consequently white, overlies a core of green. Such plants have exclusively albino offspring, since the germ cells are derived from the sub-epidermal layer which is albino. In the converse, but much rarer form of variegation (*Pelargonium*, Holly, *Coprosma*) a green skin overlies a white core, and from such plants (though experimental proof has only been obtained in *Pelargonium*) the seedlings will be all green.

Baur extended his interpretation to *Cytisus adami*[1], which has a skin of *C. purpureus* over a core of *C. laburnum*, and to the various Bronvaux Medlars, which have one or more cell layers of *Cratægus mespilus* over a core of *C. monogyna*. On the last subject a paper giving many details has lately appeared by J. Meyer (*Zts. f. Abstammungs- u. Vererbungsl.* XIII, 1915, p. 193).

The object of this note is to point out the fact that collateral evidence shows some unsuspected plants to be in reality of this nature, namely periclinal chimæras, having an outer layer or cortex distinct in genetic composition from the inner core. My attention was called to the subject by reading a report of an address of Mr C. E. Pearson to the Horticultural Club (June 30, 1914), in which he stated that some Bouvardias, and the class of Pelargoniums known as "*Regals*" did not come true from root-cuttings. Now the buds formed on true roots arise by endogenous growth from the central tissues which,

[1] It must be borne in mind that the distribution of fertility in *C. adami* has not yet been dealt with. Usually, at least, the *purpureus* flowers have bad pollen and the *adami* flowers good pollen.

pushing through the outer cortex, grow into plants exhibiting the characters proper to the "core."

Whenever therefore plants grown from root-cuttings differ from those grown from stem-cuttings, we may infer that the plant is a periclinal chimæra. As cases accumulate it will be interesting to learn the classes of distinctions by which the cortex may differ from the central tissues. Presumably they will include the various kinds of distinctions for which genetic factors are responsible. Apart from the graft hybrids, in the only examples hitherto known the distinctions have been in the presence and nature of the chloroplasts. The cortex may be white and the core green or *vice versâ*, and in Pelargonium we also know a form having the core green and the cortex in the heterozygous yellow condition[1] which Baur first identified in *Antirrhinum*. From such a plant both green and yellow seedlings have been raised here, and doubtless total albinos are also produced.

In *Bouvardia* some doubles are said to give singles from their root-cuttings, and in several cases differences in colour are reported. In answer to my questions Mr Pearson kindly wrote that the doubles said to have given singles are Alfred Neuner[2], President Garfield and Hogarth. In our own experiments with these three varieties however this result did not occur, for the products of both root- and stem-cuttings were identical. Nevertheless I see no reason for doubting the correctness of Mr Pearson's record, which is moreover supported by a statement made in general terms by J. C. C. in *The Garden*, I, 1889, p. 347 that many, if not all of the plants raised from root-cuttings of double Bouvardias will produce single flowers. The nature of the discrepancy between the two results will be considered later.

As regards distinctions in colour between root-cuttings and stem-cuttings J. C. C. (*loc. cit.*) says that he has "never known the ordinary cuttings to sport," but that he has had "many instances where, when plants have been raised from root-cuttings, all those sorts with red or pinkish-coloured blooms have reverted to the white-flowered forms[3]." In our own experiments one case only has given a positive result. Bridesmaid, a double, having the outer surface of corolla pink and the inner faces of the petals pinkish-white (see coloured plate), has given uniformly from its root-cuttings plants agreeing in every respect with the well-known Hogarth, a double carnation-scarlet[4].

[1] Plants entirely of this heterozygous yellow also exist.

[2] A writer in *The Garden*, 1916, p. 122, makes the same statement as to this variety.

[3] Cp. *The Garden*, I, 1889, p. 380.

[4] [Cf. Plate VIII, facing page 268.]

Over sixty such plants have been raised from the roots of Bridesmaid. Negative results occurred, as already stated, with President Garfield (double pink), Alfred Neuner (double white) and Hogarth itself. The evidence is so far clear that Bridesmaid is a periclinal chimæra having a skin or cortex of pinkish-white over a core of Hogarth.

The "Regal" Pelargoniums are a class of plants having flowers partially double, with a curious crumpling of the petals. We attempted to raise root-cuttings of several but failed, doubtless through a mistake in treatment. That such plants should be periclinal chimæras is exactly what one might expect. The crumpling or buckling of the petals is presumably a consequence of an unconformity of growth between the outer and inner constituents. Similar buckling of the leaves is a striking feature of Winkler's *Solanum* graft hybrid which he called *Gærtnerianum*, and I have little doubt that from root-cuttings of these Regals the ordinary flat-petalled forms will be produced, as Mr Pearson stated.

I was disposed to apply the same interpretation to a curious case quoted by Darwin (*Animals and Plants*, I, p. 384). There is a form of *Berberis vulgaris* with seedless fruit, which can be propagated by cuttings or layers, but its "suckers always revert to the common form which produces fruit containing seeds." Darwin adds that his father repeatedly tried this experiment, and always with the same result. But Duhamel (*Traité des Arbres Fruitiers*, I, 1768, p. 151) states that the seedless condition is acquired with age. The seedless variety is found wild in Northern France and on being transplanted into gardens develops seeds, though subsequently the same plants return to the seedless condition. Poiteau[1] has a passage to the same effect. I have only lately obtained the plant. Formerly it was well known under the name "Maiden Barberry," and was grown for preserves, but now it has almost disappeared from cultivation. I was fortunate in finding it with Messrs Smith of Newry, who keep it under the name *Berberis vulgaris*, var. *asperma*. It will now be further investigated. Seeing that the seedlessness is retained when the plant is propagated by "cuttings or layers" the suggestion that return of fertility is merely a matter of rejuvenescence seems scarcely probable, though pending examination one cannot assume that the "suckers" arise from roots.

Apart however from this doubtful case the distinction between

[1] *Pomologie Française*, II, 1846, s.v. *Épine Vinette Ordinaire*. The seedless fruit is figured by Nicholson, *The Garden*, I, 1889, p. 264.

cortex and core—to use non-committal terms—may relate to chlorophyll-production, doubleness or singleness of flowers, colour of flowers, size of parts (as indicated in the Regal Pelargonium). With further observation of the produce of root-cuttings the list will no doubt soon be greatly extended. There seems *à priori*, to be no reason why the distinction may not affect any factorial character. For example, both Bridesmaid and Hogarth Bouvardias are short-styled, but there would be nothing surprising if one or other had been long-styled.

Having in view the fact, which can scarcely be doubtful, that these various chimæras arose as seedlings, their peculiar constitution must be recognised as having been produced by somatic segregation. How the characters are distributed among the embryonic layers of the plants is however as yet uncertain. All that can be declared is that, in those plants which give a distinct form from their root-cuttings, the plerome is factorially distinct from the outer layers; but the constitution of the periblem as distinct from that of the dermatogen cannot be yet decided, though perhaps on this point further genetic analysis might throw light. In *Bouvardia* I have found seed-production very difficult to obtain, and hope for some more amenable subject for such investigations. It would besides be interesting to know whether somatic segregation occurs with any special frequency between the three embryonic layers—whether, in other words, these layers have any prerogative individuality in that respect. The fact that the plerome has the power, when it forms adventitious buds, of providing out of itself all the parts normally arising from periblem and from dermatogen, is manifestly beside the question here suggested for consideration.

Proof that a plant is a periclinal chimæra may of course be obtained from adventitious buds arising in internodes of the stem, as well as from those formed on roots, for such adventitious buds are also extensions from the plerome. At the time when plants with variegated leaves were much cultivated it was often observed that they (*e.g.* Zonal Pelargoniums) gave only green plants from their roots. The observation presumably applies generally if not solely to plants in which the variegation affected the skin periclinally. Moreover Hally[1] records that when the variety Mrs Pollock was propagated in such a way as to cause adventitious buds to arise from the internodes the resulting shoots were green.

[1] *Gard. Chron.* 1867, p. 1000, and 1867, p. 74; see also *Rev. Hort.* 1866, p. 429.

Meehan (signing T. M.), contributing to the same discussion[1], notes that though several variegated plants produced green shoots from root-cuttings, those raised from *Pyrus japonica*, variegated, came true. Thus far I have failed to obtain this plant and I have not met with any one who remembers it. Probably its variegation was not of the periclinal kind, or perhaps the pieces used for propagation were not true roots.

Pending further evidence it is natural to interpret these cases as examples of heterozygous plants in which there has been somatic segregation of a factor at an early stage. On a general survey of the phenomena of chimæra-production and of bud sports, the indications suggest that such a segregation may occur at many and perhaps at *any* cell divisions by which the parts of the embryo are constituted, or the organs of the plant differentiated. It may well be that segregation is most commonly relegated to the division in the germ cell cycle, but I am unwilling to regard segregation postponed to the reduction-division as a process distinct in kind from those somatic segregations of which bud sports are the visible manifestation.

At the beginning of this paper it was remarked that certain double varieties of *Bouvardia* which had been reported as giving singles from their root-cuttings did not in our experiments behave in that way. But taking the periclinal variegated plants as an analogy, just as we are familiar with the formation of solid shoots composed entirely of tissue having the characters which in the chimæra are confined to the cortex, so may the double Bouvardias have formed shoots entirely double, without any core of singleness. Wholly albino shoots for example are common on variegated plants with white cortices, being doubtless formed by periclinal divisions in the subepidermal layer. Still more frequently patches may be found in the leaves, in which the white layer is more than one cell thick. In some variegated plants, *e.g. Euonymus japonicus*, var. *latifolia*, irregularities of this kind occur in almost every stem, and totally white shoots are often produced. Similar proliferation in the layer lacking the factor for singleness might easily lead to the formation of a shoot altogether devoid of singleness, and in all probability such a shoot would be then quite indistinguishable from the form previously recognised as that of the variety, though no longer a periclinal chimæra.

[1] *Gard. Chron.* 1867, p. 952. Cp. *ibid.* 1872, p. 1321, *Pyrus japonica* said to produce *flowers* borne directly on "roots" which had been cut for propagation by cuttings. Probably the "roots" were underground stems in both cases.

Bridesmaid

Hogarth

Root-Cutting from Bridesmaid

[*Note.* November, 1916. Since this paper was written a fresh crop of Bouvardia root-cuttings has been raised. They are just beginning to flower. Those from Bridesmaid are Hogarth as before. Whether the point is significant or not I cannot say, but it may be worth mentioning that whereas in Bridesmaid the *inner* surfaces of the petals are nearly white, the outer surfaces being pink, in Hogarth the *outer* surfaces are whitish and the inner scarlet.

The Barberry mentioned in the text proved to be the ordinary form with seeds. I should be grateful to any one who can supply the genuine "*asperma*" variety. W. B.]

NOTE ON A PHEASANT SHOWING ABNORMAL SEX-CHARACTERS

(With Plate IX)

[*Journal of Genetics*, VI, 1917]

IN *Proc. Zool. Soc.* June, 1915, p. 282, Mrs Haig Thomas described a pheasant showing a curious combination of male and female characters. In view of the exceptional nature of the case we publish figures of some of the feathers in Plate IX.

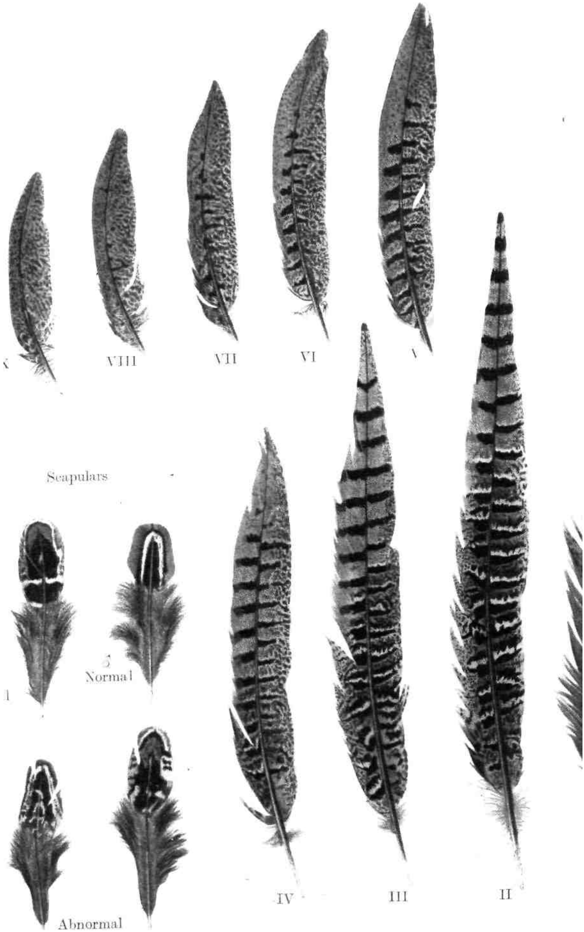
The essential peculiarity is that the two central rectrices in both colour and pattern *are of the normal male type for the basal third of their length, then female through the central third, and in the peripheral third male again.*

In the second rectrices the peripheral third is male but the rest female. The other seven rectrices are somewhat similar, but the female area is diminished in each successively, and only a trace of female pattern is perceptible in the bases of feathers external to the 5th. The male pattern is more definite and has a greater extension on the external than on the internal webs, except in the centrals, which are approximately symmetrical.

Another remarkable feature is the development of the two central under tail coverts (figured) which are specially differentiated and barred as in the hen pheasant. [In the original description these two feathers were reckoned with the rectrices which were thus stated to be 20, instead of the normal 18.]

The central rectrices seem in their development to have gone through a male stage, then a female stage, and then again a male stage. In the other rectrices there is no clear indication of a male stage corresponding with that shown by the basal parts of the centrals, but such a stage may no doubt be represented (though indistinguishable) in the base of the quills.

As regards the plumage of the body and wings the appearance is that of a male in which the secondary sexual characters are not well developed. Two scapulars are figured with the corresponding normals for male and female. In them there is no sharp distinction between male and female areas. The upper tail coverts, rump, and back approach the normal male. The feathers of the breast are for the most part male so far as their exposed ends are concerned, but the covered



VIII
VII
VI
Scapulars
Normal
Abnormal
IV
III
II

PLATE IX

parts showed traces of female pattern[1]. The head and neck are male. The two sides of the body are similar, but there is some irregularity in the degree to which the individual scapulars, wing coverts, and breast feathers fall short of the normal male colours, and the appearance of these parts of the plumage is somewhat patchy, suggesting a mosaic such as is familiar in certain moths.

The bird was dissected and found to be a male, with testes of about normal size. No trace of female organs was seen. The spurs were fully formed. The bird was bred in May and shot in January.

The significance of the phenomenon is altogether obscure. The object of the present note is simply to bring the case to the notice of geneticists. To carry the study further the first step would of course be to examine the immature stages of pheasants, for which we have no proper material. The question of hybrid origin has also to be considered. A male of *P. formosanus* was used for three years previously in the pheasant pen. The specimen is deposited in the Cambridge University Museum of Zoology.

[1] The buff ends without pattern occurring in some of the breast feathers are suggestive of female *formosanus*. (R. H. T.)

Dr KAMMERER'S TESTIMONY TO THE INHERITANCE OF ACQUIRED CHARACTERS

[*Nature*, CIII, 1919]

Professor MacBride's letter in *Nature* for May 22nd last calls for some statement from me. When, in 1910, I was engaged in writing those chapters of my book, *Problems of Genetics* (1913), which deal with the effects of changed conditions in producing genetic variation, I endeavoured to form an opinion as to the validity of the cases usually claimed in recent years as having given positive results. I had no difficulty in showing that nearly all this evidence is unsubstantial. The copious and astonishing observations said to have been witnessed by Professor Tower, of Chicago University, and by Dr Kammerer, of the Vienna Versuchsanstalt, naturally called for exceptionally careful examination. The results of both these authors had been very widely accepted, and had begun to pass current in the text-books. In the case of Professor Tower's paper, as I demonstrated in my book, close textual criticism revealed features which suggested that implicit confidence should be postponed pending confirmation—a conclusion to which I had already come when, on a visit to Chicago in 1907, I had seen illustrative specimens which Professor Tower was good enough to show me. Professor Tower's results are still quoted (*e.g.* by Babcock and Clausen in their recent text-book, 1918), but we have for some years awaited fresh light on the facts or any explanation of the difficulties to which I directed attention.

In the case of Dr Kammerer's statements, most were plainly incapable of ready verification. The instance of Alytes was the most favourable for this purpose, inasmuch as the males with the horny pads, said to have been produced in response to changed conditions, could be easily preserved. So, no doubt, might the Salamanders, of which the "*sattsam bekannte*" history, as Professor Baur calls it, has been published in numerous German periodicals; but there was this difference: that whereas Salamanders corresponding with Dr Kammerer's several patterns can be had from the dealers, students of the Batrachia are, I understand, agreed that Alytes with Brunftschwielen does not exist in Nature. I therefore wrote from Cambridge (July 17th, 1910) to Dr Kammerer asking for the loan of a demonstrative specimen, promising to examine it with every care and to return it in

due course. He replied in English (July 22nd) that he was on a holiday, continuing: "As soon as I shall be returned to my usual work—two congresses and a journey to Munich are still between—I will send to you any objects you may need for your book and have interest for, with the greatest pleasure! I hope that it will not be too late then for using them in the chapter, 'Effects of External Conditions,' of your future book.

"I am not quite sure whether I killed already specimens of Alytes with 'Brunftschwielen' or am possessing only living males of this (F_4) generation.

"But I do not doubt that also other objects are well fitted to show easily the effect of conditions and their inheritance. Especially my new experiments on influence of soil, etc., upon colours (not yet published, except some preliminary notes; for instance, in the *Verh. Deut. Naturforscher u. Aerzte*, Salzburg, 1909) are much more favourable for that purpose than the instinct variations, in spite of their morphological consequences.

"I have also promised (*i.e.* Dr Przibram has in my name) to Mr Doncaster to spare him a series of tadpoles with alterations, etc., for your museum; and it is my intention to fulfil this promise, together with that given to you in my present letter during the beginning of this autumn." Nevertheless, neither I nor the Cambridge Museum (as Dr Doncaster tells me) ever received any of the promised material.

Later in the summer of 1910 I unexpectedly was able to attend the *Mendelfeier* at Brünn, and was for some time in Vienna, having the privilege of being the guest of my old friend Dr Przibram. I was many times at the Versuchsanstalt, and inquired in vain for the Alytes. On one occasion especially, about October 3rd or 4th, I was there in company with Professors E. Baur, Lotsy, Nilsson-Ehle, Dr Hagedoorn, and the late M. Ph. de Vilmorin. Those who survive of that party will remember that, on conferring together, we all shared the same feeling of doubt. After seeing what Dr Kammerer showed us we were entirely unconvinced, and in particular it seemed to us inexplicable that, if Alytes had existed with Brunftschwielen in July, one specimen of so great a curiosity should not have been preserved, if only for exhibition with the Salamanders at Dr Kammerer's numerous lectures. I may add that I expressed my doubts categorically to Dr Przibram, the head of the Anstalt, but I am glad to think that, though he defended Dr Kammerer, our cordial inter-

ourse continued unbroken up to the time of the war. Few, I imagine, ill now consider that, on the evidence available, my scepticism was ot justified. (For an elaborate and destructive criticism of Dr Kammerer's statements, see Boulenger, G. A., *Ann. and Mag.* August, 1917, . 173.)

After reading Dr Kammerer's new paper I agree with Professor IacBride that a fresh inquiry is desirable. The two photographs, 'af. x., Figs. 1 and 2, which he accepts as proof of Dr Kammerer's bservation, present some very curious features, and I feel much uriosity concerning them. It is, of course, on Fig. 2 that the case ests. This photograph, said to be the work of Professor E. D. Conglon, of Harvard, is extraordinarily bad. It represents a Batrachian ying on its back, seen from in front. Were we not told that it is Alytes, the fact could not have been ascertained, for all but the ands is a blur. The hands are seen from their dorsal surfaces. On the radial side of the *wrist* of the right hand is a lump which Dr Kammerer claims as a Brunftschwiele. The phalanges of the thumb, as Dr Kammerer expressly declares, are unmodified in this specimen, and no *Schwielen* are visible on the left arm or hand at all. Though on analogy with other genera *Schwielen* might well occur on the wrist or forearm, the proposition which Fig. 2 is intended to support is not that set forth in the original paper which I criticised (cf. especially *Arch. Entwm.* XXVIII, 1909, Taf. XVI, where a modified *thumb* is vaguely represented). In the text of the present paper we are told that the *Schwielen* are very variable in position and extent. *I do not, however, find any mention of modification in digit iv.* This finger is, of course, external, and could scarcely function in the embrace; nevertheless, the *outer* side of digit iv is most conspicuously thickened in the right hand of the animal shown in Fig. 2. So striking is this appearance that everyone to whom I have shown the figure at first sight supposes this thickening to be the *Schwiele* illustrated. I myself, on looking at the picture before reading the details, had no doubt that this was the *Daumen* with its excrescence, the hand being thus supposed to present a palmar view. Dr Boulenger at once pointed out to me that this interpretation was impossible, for the reason, among others, that the comparative lengths of the digits proved the hand to be shown in dorsal view, and that the modified digit is iv. It must be remembered that the photograph is so indistinct that much is left to the imagination.

The peculiarity of the right digit iv would be still more manifest

if Fig. 1, which gives a normal Alytes, were a genuine photograph. It has, however, been so clumsily painted up that the extremities are not like those of any animal. Each finger and toe has a painted outline, not always in the right place, and only on comparison with actual specimens can the full extent of the modification in digit iv of Fig. 2 be appreciated. As it stands, this digit is very like the *Daumen* of the original figure. I will not yet venture on a positive interpretation, but I may remark that what the new evidence suggests is that these modifications, whatever they may be, and to whatever cause they may be due, can also appear on the outside of digit iv.

I find it difficult to understand why, if these structures are as Dr Kammerer declares, he did not make a proper series of photomicrographs of them *in situ*, showing their several positions and forms —no very hard task for such an institution as the Versuchsanstalt. Entomologists and students of fungi make such photographs constantly. Even one good ordinary photograph or drawing would have shown more than the ambiguous pictures now offered us. If anyone wishes to see how Alytes looks in a good photograph, he should turn to Boulenger (*Bull. Ac. Roy. Belg.* 1912, p. 573). The latest of Dr Kammerer's figures dates from July, 1913. A long series of *Arch. Entwm.* has been published during the years of the war, often with magnificent plates. Dr Kammerer does not state how many modified Alytes he has had, but by implication they have been numerous. If, on second thoughts, he was unwilling to send one to England, could he have resisted the temptation to send one to the Berlin Museum to be shown to Professor Baur, and so confound him and other sceptics? Three years had elapsed since we openly expressed our disbelief, but I know that up to January, 1914, no such specimen had been sent.

Professor MacBride urges that sceptics should repeat experiments on the inheritance of acquired characters. We, however, are likely to leave that task to those who regard it as a promising line of inquiry. Why do workers in that field so rarely follow up the claims of their predecessors? Each starts a new hare. Scarcely has one of their observations been repeated and confirmed in such a way that we could be sure of witnessing the alleged transmission if we were to try for ourselves. Brown-Séquard's observation on guinea-pigs is an exception. That has been repeated by various observers, until at length, by the work of Graham Brown[1], the mystery may be regarded as explained. The observation was true, but the interpretation was

[1] [*Proc. Roy. Soc.* 1912, vol. LXXXIV, B. p. 555.]

faulty. As I have often remarked, acquaintance with the normal course of heredity is an indispensable preliminary, without which no one can interpret the supposed effects of disturbance. This knowledge of normal genetic physiology is being slowly acquired, and already we have enough to show that several variations formerly attributed to changed conditions should not be so interpreted. Even in this case of Alytes, were a male with incontrovertible Brunftschwielen before our eyes, though confidence in Dr Kammerer's statements would be greatly strengthened, the question of interpretation would remain, pending the acquisition of a knowledge of Batrachian genetics.

[*Note.* A further discussion of this case will be found on pp. 378–381 of the present volume. Ed.]

THE PROGRESS OF MENDELISM

[*Nature*, CIV, 1919]

FROM the discoveries to which the Mendelian clue immediately led, many lines of research and speculation are diverging. These enterprises have still aims in common, a fact which we recognise by including all under the one name, genetics; for, though various in their methods, all relate to the physiology of breeding, a department of science the growth of which is a feature of the period surveyed on this occasion.

Stocktaking at the present moment is, however, not easy. Much of the new work is in an incipient stage, and that which is the most attractive of all—namely, Morgan's effort to establish a close connection between cytological appearances and the results of experimental breeding—promising though it is, must be tried by tests on a scale far wider than experience of *Drosophila* provides before we are able to assess its value with confidence. Whether the theory that the factors are arranged in the chromosomes, like beads on a thread, stand or fall, it has already served the purpose of a good theory. It has fired the minds of many workers, and has directed their inquiries with manifest success. Its weakness lies first in the narrowness of the field studied, hut besides this it is not yet wholly free from the objection that the subordinate and incidental hypotheses are not altogether independent of each other.

Various as are the methods of attack, the objects before us are sufficiently clear. Among them the most important is a determination of the moment or moments at which segregation may occur. To the solution of this problem most of the investigations contribute. On one hand, we have the large body of facts consistent with Morgan's view that synapsis is the critical moment. Were our outlook confined to animals, we should scarcely hesitate to accept that hypothesis as satisfying the conditions, but the plants give no such clear answer. Not only is an obvious somatic segregation leading to genetic diversity of the parts not rare, as in many variegated plants and plants which give dissimilar forms from adventitious buds, but there is now a large group in which the male and female organs of the same plant differ in the factors which they carry. Miss Saunders's stocks are the classical example, where the male side carries doubleness and cream

plastid colour, whereas the ovules are mixed in these potentialities. Similar sex-linkage, as, following Miss Pellew's use, it may provisionally be called, has been shown to exist in Petunia, *Campanula carpatica, Begonia Davisii,* and in certain forms of Œnothera.

In all such examples segregation cannot be supposed to occur later than the constitution of the sexual organs. Collins's experiment, showing that in *Funaria* the scales surrounding the male organs by their vegetative growth give rise exclusively to male mosses, is another and very striking indication to the same effect. The genetics of "rogue" peas point to a similar conclusion in regard to the distinction between the rogues and the type from which they come. In some way not yet clear, the type-elements are wholly or partially excluded from the germ-lineage of the heterozygotes, being apparently relegated to the lower parts of the stem. Such facts raise a suspicion that, considered as genetic machines, plants may be fundamentally distinct from animals, an idea already suggested by the contrast between their modes of growth. In the animal the rudiments of the gametes are often visibly separated at an early embryonic stage, whereas in the plant they are given off from persistent growing points. Indeed, since Baur's work with variegated chimæras, which led to his brilliant interpretation of Winkler's "graft-hybrids," this possibility has inevitably been present to our minds.

In knowledge of the nature of sexual difference many very substantial advances have been made, which have much extended the original discovery that sex depends on a segregating Mendelian factor, in some forms the male, in others the female, being the heterozygous member. In the fowl femaleness is dominant, and the hen is heterozygous in sex, from which Morgan drew the interesting corollary that the "henny" character of the Sebright cock is also a dominant. Not only has this been proved experimentally, but he has lately shown that after castration the Sebright cock acquires ordinary cock's plumage, much as hens do in ovarian disease. Perhaps we may regard the henny male as containing part of the large compound factor which normally constitutes femaleness. Conversely, we may interpret the spurs frequently present in normal Leghorn hens as indicating that they have lost that part of the female factor which inhibits the growth of the spur. Whether such transference involves actual detachment of chromosome material, as Morgan's theory would demand, is uncertain. Nevertheless, an approach to such evidence is provided by the extraordinarily interesting observation of Bridges

of a condition which he calls non-disjunction. Certain crosses in *Drosophila* failed to exhibit the normal sex-limitation, and unexpected terms appeared. Bridges was able to show that in the families which behaved in this way an extra sex-chromosome sometimes occurred, carried over, as he imagines, by some error of division. Not improbably Doncaster's female-producing strains of *Abraxas grossulariata*, in which evidence of an extra chromosome was found, are an analogous case. Patterson with great probability proposes a similar explanation for the curious phenomenon which he has investigated in *Copidosoma*, where, by polyembryonic division of a single egg (almost certainly), males, females, and inter-sexes may result. The inter-sexes seen by Kuttner in *Daphnia*, and those produced by J. W. Harrison with considerable regularity in some hybrid combinations of species of Geometers, are obviously to be considered in this connection, and doubtless the sterile males, accompanied by fertile females, which Detlefsen found as the normal produce of a species cross in *Cavia*, will be investigated with such possibilities in view.

But though sex behaves in so many ways as a Mendelian allelomorph, showing, of course, frequent phenomena of linkage, it begins to be remarkable that no case of crossing-over in respect of these linkages has yet been established. Were the sex-chromosome always mateless, this fact would fit admirably with Morgan's views, but since the x-chromosome not rarely has a mate, a distinct problem is created. As bearing on the same question, we have also to remember Tanaka's observation that a certain linkage found in the male silkworm is absent in the female.

Another far-reaching discovery has been made by F. Lillie. When in horned cattle twins of opposite sexes occur, the female is sometimes sterile, being called a free-martin. We were inclined to interpret these twins as arising by division of one fertilised ovum, but Lillie, in a study of material from the Chicago stockyards, found that an ovum had dehisced from each ovary, and the twins were therefore originally distinct. Moreover, he showed that in some instances the twins have an actual anastomosis in the fœtal circulation. We are thus driven to believe that the presence of a male embryo may influence—in cattle—the development of a female embryo, poisoning it, in so far that the development of the generative organs is partially inhibited.

Many complex cases of interaction between factors have been successfully analysed. Punnett's elaborate experiments on the

colours of rabbits and sweet peas, Emerson's studies in *Phaseolus*, and several more such investigations are gradually laying a solid foundation from which the mechanism of factorial determination may be deduced. The discovery made by Nilsson-Ehle, and independently by East, that in some forms there are several factors with identical powers, is another notable advance.

Controversy is proceeding respecting the divisibility of factors. When on segregation, either in the gametes of F_1 or in later generations, instead of two or three sharply differentiated classes of zygotes, much intergradation occurs, or when one of the parental types fails to reappear, the result may be interpreted either as showing imperfect segregation, or as an indication that the number of factors involved is very large. The balance of evidence perhaps suggests that many factors can, and on occasion do, break up (as the sex-factor almost certainly does), some commonly, other exceptionally, while others, again, seem to maintain their individuality indefinitely unimpaired.

As bearing on evolutionary theory, the new work leaves us much where we were. Progress in genetic physiology has been rather a restraining influence. The notion that Mendelian segregation applies to varieties and not to species has been often refuted. One of the most useful contributions to this subject is Heribert-Nilsson's evidence respecting *Salix* hybrids. Wichura believed himself to have proved that they and their derivatives are simple intermediates between the parental forms, and this statement, which has passed current for fifty years, is now shown to be a mistake due to insufficient material. Interest also attaches to Castle's recent withdrawal of his conclusion that by continued selection certain Mendelian characters in rats could be modified, an opinion which, though consistent with his own experimental work, has not stood a crucial test. We are still without any uncontrovertible example of co-derivatives from a single ancestral origin producing sterile offspring when intercrossed. This, one of the most serious obstacles to all evolutionary theories, remains. The late R. P. Gregory's evidence that tetraploid Primulas, derived from ordinary diploid plants, cannot breed with them, though fertile with each other, is the nearest approach to that phenomenon, but the case, though exceptionally interesting, does not, of course, touch this outstanding difficulty in any way.

Space does not suffice to enumerate the practical applications of genetic science to economic breeding, of which some have already matured and many are well advanced.

Linkage in the Silkworm: A Correction

[*Nature*, CIV, 1919]

In referring to Tanaka's work on silkworms I made (*Nature*, Nov. 6, p. 216)[1] a mistake which should be corrected. His discovery was not that two characters linked in the male were not linked in the female, but that in a case of linkage common to both males and females it is only in the males that crossing-over occurs. Since, on the analogy of *Abraxas*, the female is presumably in the silkworm the heterozygous sex, this observation is complementary to and consistent with Morgan's evidence that in *Drosophila* there is no crossing-over in the male, which in that animal is heterozygous in the sex-character. The paper is in *Journ. Coll. Agr.*, Tohoku Imp. Univ., VII, 1916, Pt 3. Also the forms found by Patterson associated with males and females should have been called "asexual," not "inter-sexes."

[1] [This volume, p. 279.]

STUDIES IN VARIEGATION. I.

(With Plates X—XII)

[*Journal of Genetics*, VIII, 1919]

THE phenomena of variegation due to absence or deficiency of chlorophyll have for some time been a special object of study at the John Innes Horticultural Institution. The interest of the subject lies in the circumstance that in variegated plants an opportunity is given of witnessing somatic distribution of a character, deficiency of chlorophyll, already known to be in many plants a Mendelian recessive. It is true that up to the present time no direct experimental evidence exists sufficient to prove that the characters, presence and absence of chlorophyll, heterozygously combined together in fertilisation, can actually lead to the production of a variegated zygote; but from the general course of the phenomena of mosaicism, presenting not very rarely two allelomorphic differences in juxtaposition in the same plant, we may assume without much reservation that this interpretation is admissible. Baur[1], indeed, speaking of a blue *Veronica* bearing a white-flowered branch, observed by de Vries, is disposed to refer such cases to original mutation by loss, rather than to somatic segregation of characters in heterozygous combination. Evidently there is at present no means of positively distinguishing the two possibilities, but I incline to regard somatic or vegetative segregation as on the whole the more acceptable account. If this hypothesis be the true one, we have in variegation a visible model or plan of segregation by which the properties of the germ-cells are certainly determined in many instances, and we may at least entertain the possibility that in plants segregation in properties *not* thus producing visible somatic effects may also be similarly determined. The series of examples which will be described in the present and succeeding papers illustrate miscellaneous features in this special kind of segregation. Apart from any question of wider application the phenomena are, I think, of obvious genetic importance.

PART I. *Reversal in Periclinal Chimaeras*

Variegated plants having a white subepidermal layer extending over a green core, however fertilised, give exclusively white or albino

[1] *Einführung*, &c. p. 218, *note*.

offspring, which of course die after a short existence. Conversely those having a green skin over a white core give green offspring only. The significance of this observation was first emphasised by Baur. We have seen numerous examples of such behaviour in the course of our work, of which a list will eventually be given.

The general appearance of these chimaeras, as Winkler and Baur have called them, is familiar. It is noticeable that in some of them the thickness of the "skin," whether white or green, may remain with great constancy the same over very large areas of leaf-surfaces. In white-skinned forms which are thus regular (*e.g.* Holly and Box) the deficiency of chlorophyll affects chiefly the subepidermal layer. In other plants (*e.g. Nicotiana colossea* var. *variegata*) there is continual irregularity, some leaves having only the subepidermal layer white, while in others the underlying layers are similarly affected to varying depths. In most white-skinned plants the edges of the leaves are solid white throughout their whole thickness, so that each leaf has the white marginal band characteristic of "*varietates albo-marginatae*" as they are styled in horticulture. The width of these white edges is sometimes fairly constant, but generally varies considerably.

The condition in which the core is white and the skin green is far less common, and hitherto we have seen none in which the green layer is uniformly one cell thick. Generally the edges are for a considerable breadth solid green, the thickness of the green layer diminishing towards the centre of the leaves where the white core shows through, being sometimes entirely exposed (as in *Coprosma*). Irregular bands of solid green are often prolonged from the margin into the middle of such leaves. Several of the green-skinned chimaeras have the peculiarity that their *stems* are destitute of chlorophyll or nearly so. For example, in the green-skinned form of *Coprosma*, of *Vinca major*, and of one of the Pelargoniums the stems are almost white. In the green-skinned ivy-leaved Pelargonium also chlorophyll is almost entirely absent from the stem, but, owing to a great development of red anthocyanin in the cortex, the stems are a full pink, whereas in the white-skinned form of the same plant the anthocyanin is confined to a thin layer of the cortex in the stem. In connection with this type of variegation mention should he made of another, somewhat analogous, in which the absence of chlorophyll is carried a stage further. In this, not only is the stem white, but the petioles and the centres of the leaves and stipules are also throughout their thickness destitute of chlorophyll. Of this condition I know only two perfect

examples, a *Hydrangea* and the Pelargonium "Freak of Nature" raised by Messrs Cannell. Details of these plants will be given in a subsequent paper.

The occurrence to which I wish now to call attention is a somatic change such that a sport arises in which the relative positions of the green and white parts are reversed. This phenomenon of complete reversal has now occurred in five distinct plants, *Euonymus japonicus latifolius*, *Coprosma Baueri*, and three Pelargoniums, viz. an ivy-leaved variety, and two of the zonal class, Mme Solleroi and Caroline Schmidt. In none of the examples is any evidence forthcoming as to the cause of the change, nor can any suggestion be offered as to the nature of the disturbance provoking it.

Euonymus japonicus latifolius var. *variegata*.

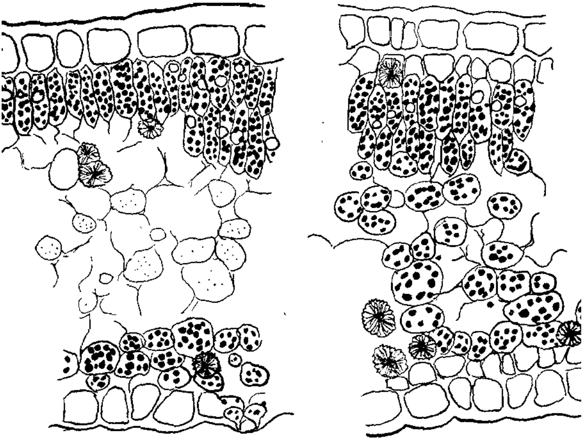
On the occasion of a visit to Messrs May's nurseries the reversed specimen was noticed among a large batch of well-grown plants of this horticultural variety. The shoot of the green-skinned form[1] was a strong branch arising in a sharply marked area of the stem, well above the level at which the cutting had been divided from the original plant. The growing point of the main stem must, at the point from which the sport arose, have formed simultaneously a white-skinned and a green-skinned segment, and in this latter area a bud had arisen which developed into the green-skinned branch. Neither among the many plants seen at Messrs May's nor among numerous specimens of the variety since examined in various gardens, including several very large plants many feet high, has any similar piece been met with. But wholly white and wholly green areas are formed not uncommonly on the white-skinned variety. If in such an area a bud is included, it gives rise of course to a branch wholly white or wholly green as the case may be. In Fig. 3[2] a leaf having such a wholly green area is shown. The green-skinned form, on the contrary, though a considerable quantity of it has now been grown, had not produced any substantial variation. In it, as in the white-skinned form, the number of cell-layers forming the "skin" is sometimes greater and sometimes less, but no white areas or white-skinned parts have appeared. The stem in this case is green.

The white-skinned form alone has flowered under observation. It failed to set with its own pollen.

[1] Mr Bintner tells me that this variety is grown in continental nurseries under the name of *Duc d'Anjou*.

[2] [The references are to Plates X—XII at the end of this paper.]

The text-figures show in section through the leaves the distribution of chlorophyll in the leaves of the two forms.



Green skin. White core. White skin. Green core.

Euonymus japonicus latifolius var. *variegata.*

Coprosma Baueri.

The white-skinned var. *variegata* of this New Zealand plant is well known. In 1877 J. Barbier figured in *Rev. Hort. Belg.* III, p. 32 the reversed or green-skinned form which had been lately brought out by Messrs B. S. Williams. To it he gave the name *C. Stocki.* It is also sometimes called var. *picturata.* A few years ago Sir William Lawrence presented to this Institution a cutting of this identical variety which had arisen at Burford as a sport from the ordinary *variegata.* The two forms are shown in Figs. 6 and 7. The distribution of the green in the green-skinned form is approximately the converse of the distribution of the white in *variegata.* Its stems however are white. The green-skinned plant has, with us, produced some wholly green shoots.

Pelargoniums.

In Pelargonium Mme Solleroi (Fig. 10) the reversal has occurred on our plants several times. Once a whole branch of green-skinned leaves was formed, for the most part as in Fig. 12, but amongst them a leaf appeared having the whole of one side green as shown in Fig. 14. On another plant of Mme Solleroi a shoot appeared bearing many leaves which were wholly white, but the leaf standing lowest on the shoot, viz. the first leaf from the stem, had the structure shown in Fig. 13, half being white and the other half green over white. In individual leaves patches of reversal have been formed as in Fig. 11. Such green-skinned patches include, I believe, always some part of the leaf-margin, and on their internal boundary they are delimited from the white-over-green parts by a white band indicating that in the area in which the two kinds of arrangement abut on each other, the deficiency of chlorophyll extends below the subepidermal layer (compare Fig. 16).

It is a peculiarity of Mme Solleroi that, so far as I have observed, no flowers are formed on the white-skinned parts, but the green-skinned branch produced a truss of pink flowers. These flowers however were ill-formed[1] and destitute of pollen. The pistils were, I believe, also deformed, but by inadvertence no note of their condition was made.

On a large pink-flowered ivy-leaved Pelargonium reversal has also occurred sporadically. Most often the reversal is confined to a part of a leaf, usually *the whole of one side* (as in Fig. 9), but more than one whole branch of the reversed kind has independently appeared. Flowers on the white-skinned parts are fertile, producing (as such plants habitually do) long white carpels in the fertilised fruits, but the green-skinned form has not yet flowered.

The white-skinned Pelargonium Caroline Schmidt very often produces wholly green sports. We have here had also several individual leaves on this variety as shown in Fig. 16, composed of a mosaic of the typical and reversed kinds, but hitherto no reversed shoot.

The phenomenon of reversal is evidently rare and exceptional. No

[1] *Note.* The variegated Pelargonium "Freak of Nature" mentioned above (stem and centres of foliar organs white; edges of foliar organs green) bears deformed flowers having both male and female organs aborted. But sports occur some wholly green, others wholly white, and the flowers on both these are perfect, ripening seed on self-fertilisation, and producing seedlings respectively wholly green or wholly white. This plant has had one small green-skinned branch which has not yet flowered.

example other than those enumerated has yet been seen among the many white-skinned plants grown here or examined elsewhere. We have, for instance, several hundred yards of *Euonymus radicans* var. *variegata* used as an edging-plant. Wholly green shoots are common on this plant, and wholly white shoots not rare, but no reversal has yet been seen. Among many hedges of white-skinned holly also no reversal was found.

Cases superficially mistakable for reversals are not uncommon in various plants. For example, in the white-skinned Pelargonium used by Baur in his observations (of which he kindly gave me a cutting some years ago) leaves like that shown in Fig. 15 occasionally appear. At first sight the condition recalls that of Figs. 11 and 16, but on closer examination this is seen to be due in reality to the formation of small solid green areas associated with irregularity in the number of layers devoid of chlorophyll. In this variety, as in many white-skinned forms, the appearance of wholly green areas is not very rare.

Obviously the occurrence of reversal, and of areas wholly green or wholly white, are consequences of some instability arising in the growing point, but there is nothing to indicate the cause of such instabilities. The formation of wholly green areas in white-skinned plants may no doubt be described as a bursting out of the green core, and might be attributed to some greater vigour of the green parts, but these expressions are merely descriptive. Injury may be suggested as a probable cause. White shoots do indeed arise with special frequency round old scars on the boles of white-skinned hollies, but green shoots, which might be expected to burst through, are extremely rare, if they occur at all in such places. The suggestion of injury is plainly inapplicable to such cases as the Pelargoniums described in this paper.

It would be interesting to ascertain whether the green-skinned forms ever change back again, and the absence of any example of this transformation may be worth noting.

As mentioned in introducing the subject, the consequence of somatic reversal is that the genetic properties of the plant are completely changed. Naturally this fact leads to a surmise similar to that suggested by the behaviour of root-cuttings[1]. In the variegated chimaeras we can visually distinguish the properties of the cortex, but is it not probable that similar genetic distinctions may exist

[1] See "Root-Cuttings, Chimaeras, and Sports," *Journ. Gen.* VI, 1916, p. 75. [This vol., p. 264.]

which are *not* thus visible? May not the phenomenon of reversal exist in regard to them also, bringing into the cortex, and so into the germ-cycle, properties previously contained only in the deeper layers?

EXPLANATION OF PLATES X—XII

The drawings from which these plates were prepared were made by Mr C. H. Osterstock. The various tones of green depend on the number of layers which are green or white respectively.

Fig. 1. *Euonymus japonicus latifolius*, white-skinned variety, having a green core.

Fig. 2. Reversed form of the same, having a green skin over a white core.

Fig. 3. Leaf from another bush of the same having one side wholly green and the other side white-skinned. (Slightly too blue in tone: Fig. 4 correctly gives the colour of the dorsal surfaces.)

Figs. 4 and 5. Back and front of a leaf of the same having an area wholly green appearing next the midrib on one side.

Fig. 6. *Coprosma Baueri* var. *variegata*; the white-skinned form.

Fig. 7. The same; green-skinned form.

Fig. 8. Ivy-leaved Pelargonium showing the mixture of the two kinds of chimaera.

Fig. 9. Leaf of the same: one side white-skinned, the other side for the most part green-skinned.

Fig. 10. Madame Solleroi, zonal Pelargonium: the white-skinned form. (The veins in this figure are too wide. They are correctly represented in the other figures.)

Fig. 11. The same with reversed areas at apex of leaf.

Fig. 12. The same: green-skinned leaf.

Fig. 13. The same: leaf all white on one side, green-skinned over most of the other side.

Fig. 14. The same: leaf half green and half green-skinned.

Fig. 15. Baur's white-skinned zonal: leaf showing irregularities in the number of layers deficient in chlorophyll.

Fig. 16. Zonal Caroline Schmidt: leaf with two separate areas of reversal.

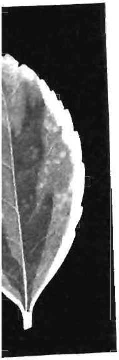


Fig. 1.

Fig. 2.

Fig 3.

Fig. 4.

Fig. 5.

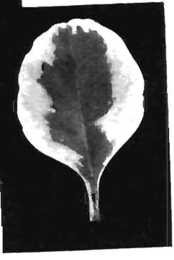


Fig. 6.

Fig. 7.

OLLEGE AND RESEAR

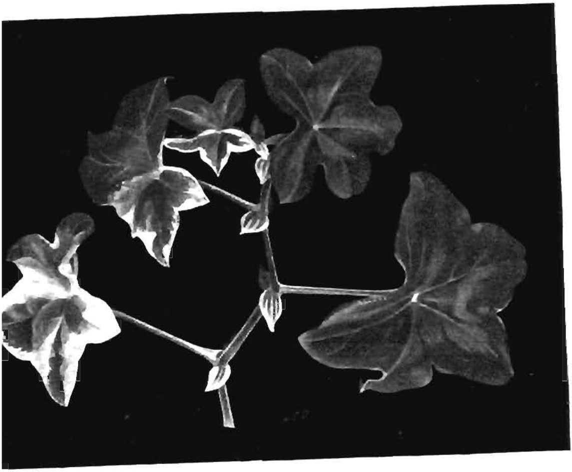


Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

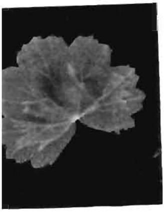


Fig. 12.

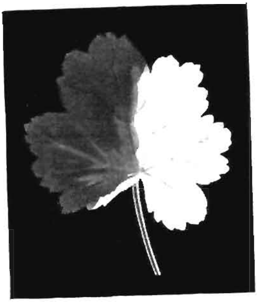


Fig. 13.

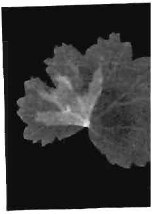


Fig. 14.

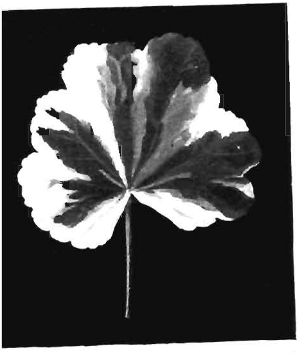


Fig. 15.

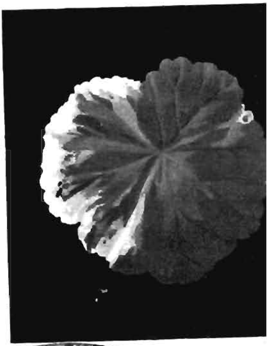


Fig. 16.

RESEARCH INSTITUTE

DOUBLE FLOWERS AND SEX-LINKAGE IN *BEGONIA*

(With Plate XIII)

[*Journal of Genetics*, VIII, 1919]

BEGONIAS are monoecious plants, having their flowers arranged in axillary cymes. In normal plants the flower which terminates each dichasium is a male; and, in the simplest arrangement, upon either side of this stands a female. For one or both of these females may be substituted a continuation of the inflorescence, which again at each dichasium ends in a male, this system being indefinitely repeated.

Since doubleness affects only those flowers which stand terminally, being that is to say in normal plants *males*, an investigation of the inheritance of this condition offered attractions, as being not unlikely to throw light on the genetics of sex. In passing it may be remarked that since a female flower can be replaced by an inflorescence, whereas a male flower is not thus replaceable, from these morphological relationships we are led to infer that the female flower contains something that the male has lost. The male flower may be thus compared to a recessive, dropped out of the inflorescence which can be produced further in the heterozygous state.

The investigation was begun in 1908 by fertilising the normal female flowers of double Begonias with pollen from singles of unknown origin. Subsequently further crosses were made between doubles and a horticultural strain of singles which was declared to have bred true for some generations. The results have been full of complications such that, after many years' work, it has become evident that no simple factorial scheme is followed, and that segregation in regard to single and double flowers must in these plants be a process liable to considerable irregularity. In general the single is a dominant as Bond also found. The recessive doubleness reappears in F_2, but the numerical proportion of F_2 doubles is low and fluctuates widely. There are many transitional forms which render accurate classification and enumeration impossible, and not very rarely several of them may appear on the same plant. Some of the more interesting of these forms will be spoken of later.

An average of many F_2 families gives about 1 double in 32, but in several large families no doubles at all appeared, and this average

has certainly no general significance. From F_1 plants crossed back reciprocally with various doubles, similar irregular numbers were obtained and no approximation to analysis could be made. To render the composition of these families intelligible lengthy descriptions would be required and little purpose would be served by the publication of such details. Their interest lies chiefly in their value as an indication that in regard to a character which in so many plants is distributed genetically according to strict allelomorphic rules, great irregularity may elsewhere prevail. Whether this irregularity is in any way connected with the monœcious structure of Begonias cannot of course be declared. Such a conclusion is by no means improbable.

The purpose of the present paper is to make known a curious discovery which resulted when *Begonia Davisii* was brought into the series of experiments. The plant is one originally found in Peru by Mr Davis, collector for Messrs Veitch, and first flowered by them in the year 1876[1]. Inasmuch as this is a real species, breeding perfectly true on self-fertilisation, it seemed suitable for use as a reliable single for crossing with doubles. When however these crosses were made it was found that any double fertilised by pollen of *B. Davisii* gives *only double-flowered offspring*—405 plants have been thus raised, and of these only 18 are recorded as having less than complete doubling. The male side of *Davisii* is therefore exclusively double-bearing. Since the same plant fertilised with its own pollen gives only singles, the female side must be inferred to be exclusively single. Tested however with the pollen of a double, it gave a result which we cannot satisfactorily interpret. Fertilisation with pollen of doubles cannot always be accomplished, since thoroughly petalodic flowers do not produce pollen. A good many doubles nevertheless when starved or poorly grown do produce anthers and pollen, as for example the well-known double called in horticulture *Begonia Lloydii*. *B. Davisii* ♀ fertilised by *Lloydii* ♂ gave 72 thorough singles and 42 with traces of petalody, a condition we have not yet seen in *Davisii* itself. The genetic nature of these slightly petalodic plants is not clear. If they can be formed when the pollen of *Lloydii* is used, we should expect them to appear when *Davisii* is fertilised with its own pollen, for this pollen used on doubles gives scarcely anything but extreme doubles. Slightly petalodic plants came also occasionally, among large numbers of singles, in families raised from *Davisii* female fertilised with pollen of heterozygous plants (F_1 from double × single ♂). When the pollen

[1] See Wynne, *The Tuberous Begonia*, 1888, p. 16 and *Bot. Mag.*, t. 6252.

of *Davisii* is used on such F_1 plants the proportion[1] of recessive, double-bearing ova, of course appears; and since perfectly reliable pollen of doubles is difficult to obtain, the pollen of *Davisii* may be substituted for it.

After discovering the peculiar genetic constitution of *Davisii* we naturally expected that the results of reciprocal crosses made between doubles and F_1 plants (from double × single) would at least sometimes show linkage of doubleness with either the male or the female side. For this investigation a considerable amount of material is now available and we are satisfied that in general heterozygotes do not show any regular phenomenon of this kind. In contrast however to the usual absence of consistent sex-linkage, one plant raised from the female side of *Davisii* fertilised by *Lloydii* was proved to possess such sex-linkage, though less complete than that of *Davisii* itself. The plant, self-fertilised, set badly and only 2 plants (singles) were thus raised. As regards its female side we have the evidence that with *Davisii* pollen it gave 11 singles, and with *Lloydii* pollen 5 singles and 1 slightly petalodic, from which it may be inferred that the ovules were at all events predominantly single-bearing. The male side tested on *Lloydii* gave 27 doubles, 14 half doubles and 5 slightly petalodic (see Nos. 23–26 in Table on p. 297).

As to the presence of sex-linkage in other heterozygous individuals the evidence is as yet conflicting. Some plants show it, whereas others do not, and we cannot as yet perceive any circumstance either in the way in which the plants were made up or in any other respect which accounts for these differences. We give in the Table (Nos. 31 to 45 on p. 297) specimens of these various behaviours.

The case naturally recalls other examples in which sex-linkage has been observed in plants. In three of these the male side has been specially distinguished as being associated with the *recessives*, though whether this is an accidental circumstance due to the way in which the plants were originally bred cannot yet be declared, but in *Petunia*, as shown by Miss Saunders singleness, the dominant, was carried by all the pollen grains, and by some only of the ovules of the single-flowered plants. In *Matthiola* the pollen was all double and for the most part carrying cream plastid-colour (Saunders); and in a plant of *Campanula carpatica* and its descendants, the pollen bears white flower colour and femaleness, the factors for blue and for the hermaphrodite condition being carried by the ovules (Pellew). In this case

[1] This proportion, as Table II exemplifies, is apparently quite irregular.

as in *Begonia* the sex-linkage was not general but special to a particular plant and its descendants. Of these examples the plastid-colour is the only one in which the converse combination has yet been built up, though perhaps the others may hereafter be obtained[1].

The condition in *Œnothera "velutina"* described by de Vries must be very similar, the recessive dwarf character being carried by the pollen. In the corresponding case of *Œnothera "læta"* the evidence also points to the pollen being all dwarf, and to the existence of a mixture of talls and dwarfs among the ovules, in spite of which the plants do not throw dwarfs on self-fertilisation. This absence of dwarfs on selfing constitutes a puzzle exactly like that of the presence of slightly petalodics in *Davisii* × double ♂[2].

When in hermaphrodite flowers the male and female sides are genetically distinct we feel fairly sure that the segregation of these allelomorphs occurs not later than the formation of the anther-rudiments, but in *B. Davisii* it presumably happens even earlier and not later than the formation of the male flowers. Those who incline to regard the reduction-division as the stage at which alone segregation can be effected may no doubt be tempted to suggest that in *B. Davisii*, for instance, pollen grains bearing the dominant factor are in reality formed but in some unexplained way fail to take part in fertilisation. As a mere suggestion of a possibility that theory cannot as yet be absolutely excluded, but in this special example it is more than usually difficult to accept, since the pollen of *B. Davisii* is to the eye exceedingly uniform and regular. There are none of the shrivelled grains which are generally looked upon as the bearers of missing elements. Though less significant, the absence of seeds partially defective is also noticeable.

In applying the term sex-linkage to such cases as this I am following the suggestion made by Miss Pellew in her discussion of "Types of Segregation[3]." The propriety of the comparison between the

[1] Since in the original form the ovules were mixed and the pollen was all recessive, the "converse" might appear in one of two forms. Either (1) the ovules might be all dominant and the pollen mixed; or (2) the ovules might he mixed and the pollen all dominant. As Miss Saunders's plants were tested, by self-fertilisation and not hy crosses with recessives, it cannot yet be declared which of the above possihle constitutions they possessed, but she considers there is a presumption that they were really arranged on the second of the two plans. (See Saunders, *Journ. Gen.* IV, pp. 332 and 359 and compare Pellew, *Journ. Gen.* VI, p. 320, etc.)

[2] For a discussion of these *Œnothera* cases see W. Bateson, *Problems of Genetics*, 1913, p. 113.

[3] *Journ. Gen.* VI, 1917, p. 319.

association of a character with one of the sexes in the case of a hermaphrodite plant and the phenomenon in bisexual animals commonly called sex-linkage may be questioned, but until we know more precisely how sex in animals is related to the phenomena in the flowering plant, no unjustifiable assumption is made and no serious confusion can be caused by their use. If, following one method of interpretation, we regard pollen-mother cells, being the latest diploid stage, as the equivalent of male animals, we can reasonably speak of the character—here doubleness—carried by the pollen grains, as *linked with maleness*, and *singleness as linked with femaleness*. The comparison, though not certainly valid is at present defensible. The relation of the hermaphrodite to the diœcious condition, whether in animals or in plants, has not yet been represented by any factorial scheme which is thoroughly satisfactory. On a survey of the various sexual arrangements followed among plants we meet a difficulty in attempting to choose any fixed moment common to all the cycles, which can serve as a starting-point for the institution of homologies. The difficulty is intensified when we proceed to the case of animals. One obvious suggestion is that the reduction-division provides such a common fixed point. Though I am not disposed to look upon that event as the only occasion on which Mendelian segregation is effected, I readily agree that many segregations presumably do happen then, especially that by which sex is usually determined among animals. Such observations however as those of the Marchals and the new evidence discovered by Collins[1] show almost beyond question that even within the group of Mosses sex-segregation may occur at different moments in the different cycles.

With equal propriety we may regard the actual gametes as the fixed point common to all and therefore homologous in all the cycles, but we have still to face the difficulty that such a critical segregation as that which determines sex (and probably others) may be sometimes effected at the reduction-division, sometimes before it, as at least in monœcious flowering plants, and sometimes after it as in Collins's *Funaria*.

The facts practically drive us to the conception that the ordinal position of the reduction-division can be shifted in the cycle, and that segregations which in some cycles precede reduction are in other cycles postponed until reduction has been already undergone. The problem is not unlike that so often raised by the differentiation of parts

[1] *Journ. Gen.* VIII, 1919, p. 139.

composing a meristic series. In one Lizard the *n*th vertebra carries the pelvis and undergoes special modification. In another Lizard the vertebra thus differentiated is the $n + m$th in ordinal series. Morphologists have long discussed whether in allotting homologies among vertebræ we should be guided by the differentiations, or by the ordinal positions. When once the true nature of segregation and differentiation is understood the question is seen to lose all significance[1], and having no precise meaning is incapable of being answered. For the *individuality of the segments is not respected* or *maintained in* variation, nor are differentiation and numerical change necessarily interdependent. We may easily satisfy ourselves that the numbers may vary and that within considerable though unascertained limits the functions and differentiations of the segments may be redistributed. I can scarcely doubt that we must similarly interpret the series of divisions and differentiations of which the life-cycles consist.'

In the Tables we represent the plants as of five classes. *Singles* are those in which the male flowers have not been seen to have more than the four normal petals. The *slightly petalodic* class have generally one or two, though occasionally rather more extra petals or petalodic anthers. These two classes cannot be quite strictly instituted, and plants having flowers of both kinds are common. The *half-double* class rauges from the slightly petalodic to the really double, but nevertheless it is a fairly uniform class. *Doubles* and *full doubles* are not essentially distinct, but the term *full* was applied only to flowers in which the petals were very numerous and close.

As was stated above, peculiar and transitional forms are common. In particular some difficulty is caused by structures consisting of female and male flowers imperfectly resolved from each other[2]. Such flowers can generally be recognised by examination of the bracts, but when this condition of imperfect resolution is combined with some degree of petalody the degree of doubling cannot be determined with much confidence.

Since double flowers stand terminally, that is to say in the male position, we supposed at the beginning of these experiments that double flowers were necessarily petalodic males. Happening however to examine the variety called Graf Zeppelin, we were struck by the fact that the double flowers, though terminal, are in reality modified

[1] See *Problems of Genetics*, p. 66.

[2] *Noticed by Bond, Journ. Gen.* IV, *1915, p. 341.*

males. There is no inferior ovary, but at the bases of the petals are iasses of exposed ovules[1]. This arrangement is normal for the variety nd gives it a most characteristic appearance. Further search among ouble Begonias showed that many are in essentially the same ondition, though the amount of ovules developed varies greatly. robably most of the fine exhibition blooms are modified female owers, though in them the ovular tissue may be reduced to a mere 'ace at the base of occasional petals.

Whether any of these plants are altogether incapable of producing ıtbers, however much they may be starved, we do not know. Our cperience inclines us to think that some plants cannot produce ıthers, though we have certainly seen thoroughly double flowers of ıe ovule-containing kind on plants which had borne double males ontaining anthers. But apart from this question we can easily cognise a class of doubles, of which *Lloydii* is a good instance, in hich the double flower is essentially male; and though they may be irly perfect doubles when well grown, this kind of double can adily be starved into producing pollen. The view that plants, *e.g.* raf Zeppelin, in which the terminal flowers are female, instead of ale as normally, may be *homozygous* females is rather attractive, but e see no means of testing it; nor if such an idea could he entertained, ould it at all account for the fact that in a full double which must rtainly be accepted as a recessive, homozygous in doubleness, the ormal female flowers standing in the lateral positions are single. eyond this point we see as yet no means of pursuing the analysis.

Since *B. Davisii* is a genuine wild species and bears exclusively ngle flowers, the conclusion to which our observations have led us, ımely that its male side is genetically *all* double, seems not a little markable.

[1] Flowers having this structure were referred to by Wynne, *loc. cit.* p. 13, and parts them are figured by Bond, *Journ. Gen.* IV, Pl. XVI. Their morphology is obscure, ıt it seems natural to regard the carpellary walls as represented by a mass of petals. e have never seen a normal female standing in the male position.

DETAILS OF EXPERIMENTS RELATING TO *BEGONIA DAVISII*

	Reg. no.		Single	Slightly petalodic	Half double	Double	Fully double
1	—	*Davisii* selfed, 4 families, 200–300 raised all true to type					
2	—	*Lloydii* selfed, 45 true					
		Various doubles fertilised by Davisii ♂					
3	—	*Lloydii* × *Davisii* ♂	—	—	—	—	32
4	49/13	Graf Zeppelin × do.	—	—	—	—	28
5	20/14	49/13 (as above) double × do.	—	—	6	3	16
6	30/15	20^9/14 (as above) double × do.	—	—	3	—	14
7	28/13	A double × do.	—	—	—	—	139
8	4/14	28/13 (as above) double × do.	—	—	9	8	78
9	30/18	A double × do.	—	—	—	—	13
10	22/14	Argus × do.	—	—	—	—	17
11	25/14	Hollyhock × do.	—	—	—	—	8
12	27/15	Louis Boucher × do.	—	—	—	—	7
13	85/18	Fleur de Chrysanthème × do.	—	—	—	4	—
		Davisii ♀ fertilised by double					
14	10/17	*Davisii* ♀ × *Lloydii* ♂	72	42	—	—	—
		Reciprocal crosses with a half double					
15	4/17	*Davisii* × 3^7/14 half double	39	15	—	—	—
16	5/17	3^7/14 half double × *Davisii*	—	3	2	17	109
17	15/15	The same half double 3^7/14 selfed	1?	28	49	—	8
		Reciprocal crosses with a heterozygous single					
18	41/16	*Davisii* ♀ × 2^{21}/14 heterozygous single	105	1	—	—	—
19	3/17	2^{21}/14 heterozygous single × *Davisii* ♂	68	14	5	17	23
20	42/16	The same heterozygous single 2^{21}/14 selfed	42	4	—	—	—
21	2/17	2^{20}/14 heterozygous single × *Davisii* ♂	67	9	4	34	24
22	36/16	The same 2^{20}/14 selfed	45	10	4	1	1

The following are tests of two plants bred in Experiment No. 14, *Davisii* ♀ × *Lloydii* ♂. In the first group 10^2/17, a *single*, was used: in the second group 10^5/17, a *slightly petalodic*, was used. In both, the male side proved to be predominantly double.

PLATE XIII

AGRICULTURAL COLLEGE AND RESEARCH INS
COIMBAT

	Reg. no.		Single	Slightly petalodic	Half double	Double	Fully double
23	12/18	$10^2/17$ × *Davisii* ♂	11	—	—	—	—
24	13/18	*Davisii* ♀ × $10^2/17$	6	—	—	—	—
25	14/18	$10^2/17$ × *Lloydii*	5	1	—	—	—
26	15/18	*Lloydii* × $10^2/17$	—	5	14	14	13
27	20/18	$10^5/17$ × *Davisii* ♂	14	8	—	—	—
28	22/18	Do. × *Lloydii* ♂	2	2	1	—	—
29	23/18	*Lloydii* × $10^5/17$	1	1	5	—	11
30	24/18	Graf Zeppelin (fully double) × $10^5/17$	—	—	1	—	—

Experiments illustrating behaviour of various heterozygous singles ($33^1/17$, $17^1/17$, $16^2/17$, $34^1/17$).

In $33^1/17$ the single factor went in from the mother's side, and there is a clear indication that the pollen was predominantly double; but in $17^1/17$ and $16^2/17$, similarly bred, the pollen was predominantly single. In $34^1/17$, the exact reciprocal of $33^1/17$, the single factor went in from the father's side, and the numbers though insufficient, do not suggest sex-linkage.

	Reg. no.		Single	Slightly petalodic	Half double	Double	Fully double
31	71/18	$33^1/17$ selfed	45	6	—	—	—
32	72/18	Do. × $7^1/17$ double ♂	43	7	6	2	—
33	73/18	$35^8/17$ double × $33^1/17$ ♂	31	25	27	2	43
34	53/18	$17^1/17$ × *Lloydii* ♂	18	—	—	—	—
35	54/18	*Lloydii* ♀ × $17^1/17$	4	2	—	—	—
36	56/18	$35^6/17$ double × do.	4	—	1	1	3
37	57/18	$35^7/17$ double × do.	41	8	2	2	7
38	34/18	16^2 selfed	27	—	—	—	—
39	35/18	Do. × *Lloydii*	55	17	—	11	17
40	36/18	*Lloydii* × $16^2/17$	88	24	—	3	3
41	37/18	Graf Zeppelin × do.	56	7	1	—	4
42	38/18	$35^{10}/17$ double × do.	55	23	15	—	14
43	74/18	$34^1/17$ selfed	73	4	—	—	1
44	76/18	Do. × $35^9/17$ double	47	16	11	—	16
45	75/18	$35^9/17$ double × $34^1/17$	6	2	3	—	1

Plate XIII shows the flowers and leaves of *Begonia Davisii*.

THE GENETICS OF "ROGUES" AMONG CULINARY PEAS (*PISUM SATIVUM*)

[*Proceedings of the Royal Society*, B, XCI, 1920]

IN 1915 we described observations and experiments on rogue peas[1]. Our results up to the end of 1914 were as follows:

(1) Rogues arise sporadically from self-fertilised seeds of various races of typical high-class peas.

(2) These rogues are characterised by pointed leaflets and upward-curving pods. Their foliar organs, stipules, leaflets, sepals, petals, and carpels are all narrower than those of the types. It is especially characteristic of rogues that their leaflets end in *points* instead of the emarginate apices proper to the types. Their seeds are, on an average, slightly smaller. Such plants have a curiously wild appearance, which contrasts greatly with the ampler proportions of the types.

(3) Rogues, self-fertilised, produce rogues exclusively.

(4) Rogues crossed with types, whichever way the cross be made, give F_1 plants which as seedlings show evident indications of the type-characters, having parts much larger than those of rogues at the same age. But these plants at an early stage, usually at some node below that at which the first flower is borne, *change to rogues*, producing stipules, leaves, and eventually pods, like those of rogues.

(5) The offspring produced by the self-fertilisation of these F_1 plants are *exclusively rogues*. In some way unexplained the type-characters contributed, whether by the father or by the mother, are excluded at an early stage, so that they do not reappear in the germ lineage.

In the variety which we have chiefly studied, Sutton's Early Giant (a strain of the well-known Gradus), plants intermediate between types and rogues are not uncommon. We have scarcely ever seen such plants in other varieties. In them a change in the foliar parts occurs like that described in the F_1 plants; but though most frequently completed at or near the first flowering node, their transformation may be deferred to a much higher level. On such plants the shape of the pods also often changes progressively, lower pods being straighter and upper pods curved like those of rogues. These intermediate plants form a fairly definite class, though they grade insensibly into both the types and the rogues. In recording breeding

[1] [This volume, p. 236.]

results we have classified the plants into a graduated series of five groups, but for the present they may be reckoned as of two kinds: (1) those in which none of the leaflets have points; and (2) those in which pointed leaflets sooner or later appear. This in practice forms a convenient distinction which can almost always be applied. The two groups thus distinguished on somatic characters differ essentially in their genetic properties: "non-pointed" plants give on self-fertilisation what in previous publications we have called *A* families, consisting predominantly of types, or at least non-pointed plants, but the "pointed" give *B* families containing predominantly rogues. Families in which the proportion of the two kinds approaches equality occur but rarely.

Intermediate plants of composite or mosaic nature are not very uncommon, and the mosaicism may be of varying extent. In extreme cases, a whole branch may differ from the main stem, and a "pointed" branch giving a *B* family may arise from a "non-pointed" main stem giving an *A* family, or *vice versâ*. The adequate discussion of these irregularly composite plants must be deferred.

We have been chiefly occupied with a study of the genetic peculiarities connected with the gradual and regular assumption of the rogue characters by the intermediate plants which sooner or later acquire pointed leaflets. From the fact that the change was progressive, we surmised that if the position of origin of the seeds on such plants were determined, it would be found that the few non-pointed plants which they produce would be found to come predominantly from seeds in the lower pods, and the pointed from the upper pods. As the result of a preliminary trial we found that this rule was in fact followed, and this observation was published[1] at the end of 1915. Further experience has abundantly confirmed it.

But the converse conclusion which we also announced at the same time, to the effect that in the case of *A* families containing only a small number of rogues these come predominantly from the upper pods, has proved to be erroneous. In families where the pointed plants are proportionally few, the seeds from which they come are not derived from any particular level on the parent plants, and the observation on which we relied was only an accident of the special case.

Since the publication of these first results the work has been continued along several lines. Having established the fact stated above, that in the *B* families the non-pointed plants come chiefly from the

[1] *Proc. Roy. Soc.* B, LXXXIX, p. 174. [This volume, p. 259.]

bottom pods, we endeavoured to ascertain more exactly the positions from which they do come. Choosing, therefore, a number of intermediate plants which we thought likely to throw *B* families, we emasculated each flower on the stems in succession, as far as possible, pollinating them from type plants belonging to families which had been selected as being the most rogue-free[1]. Since, thus fertilised, every egg cell genetically rogue will produce a rogue, and every egg cell genetically type will produce a type, the resulting family, sown in order, will show the distribution of the rogue- and type-characters among the egg cells of the intermediate parent. The seeds from each pod were sown separately, and we expected to find that the non-pointed would come almost exclusively from the lowest pods. This expectation, however, was not borne out by the result, for the proportion of non-pointed among the egg cells did not diminish noticeably at least up to the tenth flower. Since the same plants, if self-fertilised, very rarely produce a non-pointed plant from flowers higher than the fourth, a presumption was raised that the male and female sides must be differently constituted, and that the proportion of pointed gametes would be found to change with the level much more rapidly on the male side. Tests were therefore instituted, using pollen of the successive flowers of the intermediate plants and trying it on the ovules of types. The experiment has not been made on a scale sufficient to determine the true average ratios of non-pointed to pointed in successive flowers, but that the proportion of pointed increases rapidly from about the third flower is clearly proved.

Work of this kind is exceedingly laborious, and the wastage from various causes must inevitably be very large. Of the plants chosen for operation some necessarily prove to be of the wrong kinds, throwing, for example, all rogues, and all the work done on such plants turns out in the following year to be inapplicable. We considered ourselves fairly fortunate in having raised 1016 cross-bred plants from which to estimate the output of the female side, and 468 plants derived from the male side of the pointed intermediates, together with 1572 plants from flowers of known position self-fertilised[2]. The results are set out

[1] The proportion of rogues (or, more strictly, pointed) thrown by ordinary types is, in our experience, about 2 per cent. In the purer type-families selected for crossing the percentage would be even lower than this, so that for practical purposes they may be regarded as rogue-free.

[2] An attempt was made on a considerable scale, by sowing the peas of each pod in their original order, to test whether there is any orderly arrangement of the seeds. This work, which added greatly to our task, led to no positive result.

in Table I, where the actual numbers from each flower are given with the ratios deduced from them. As to the female side of the flowers the evidence may be regarded as significant up to the 14th flower. The proportion of non-pointed female gametes remains about constant at a ratio of rather more than 1 in 2 up to the 10th flower, above which it diminishes. On the male side the proportion of non-pointed gametes is about 1 in 5 for the first two flowers and then drops sharply and progressively in succeeding flowers, falling again suddenly after the 5th flower. We are satisfied that the record for the 8th flower is quite abnormal, and may be disregarded. Further observations will no doubt modify the figures here given, but the general trend of the results is unmistakable.

TABLE I. *Offspring of Pointed Intermediate Plants (selfed or crossed with type) grouped according to the ordinal position of the flowers from which the seeds were taken*[1].

Ordinal no. of flower	Cross-fertilised						Self-fertilised		
	Type-father			Type-mother					
	Non-pointed	Pointed	Ratio	Non-pointed	Pointed	Ratio	Non-pointed	Pointed	Ratio
1	57	54	1 : 1·09	9	42	1 : 4·6	18	269	1 : 15·0
2	30	42	1·4	17	83	4·9	21	240	11·4
3	65	46	0·7	8	56	7·0	18	231	12·8
4	56	64	1·1	3	30	10·0	15	228	15·2
5	32	46	1·4	7	86	12·3	4	218	54·5
6	26	37	1·4	2	59	29·5	—	144	—
7	48	43	0·9	1	23	23·0	1	91	—
8	34	41	1·2	6	28	4·6	—	71	—
9	34	46	1·3	—	8	—	—	—	—
10	25	27	1·1	—	—	—	—	—	—
11	10	31	3·1	—	—	—	—	—	—
12	15	23	1·5	—	—	—	—	—	—
13	10	23	2·3	—	—	—	—	—	—
14	5	27	5·4	—	—	—	—	—	—
15	2	8	—	—	—	—	—	—	—
16	3	3	—	—	—	—	—	—	—
17	2	1	—	—	—	—	—	—	—
	454	562	1 : 1·2	53	415	1 : 7·8	77	1492	1 : 19·4

[1] The material used in this Table is necessarily somewhat heterogeneous. It includes offspring of plants which, whether selfed or crossed, have given at least one plant as high as Class 3. To have extended it lower would have involved the inclusion of families from plants giving all rogues, and such plants could not exhibit the gradational effect which would thus have been to some extent masked. Nevertheless,

The series on the female side is much longer, because the fertilisations were largely done in 1916, a year in which the plants grew very tall. The height of a plant depends greatly on the weather, and in 1917–19 short plants were the rule. Naturally it can only be on tall plants that the contrast between the composition of the offspring derived from the lower and the upper pods can be fully displayed.* In Table II a number of such families are set out. To save space and labelling the pods were generally grouped into three or four successive lots. This was done before we set about determining the actual ratios for each flower, and though the numbers are not available for that purpose, they provide a larger total of observations than could have been reached had the material been more subdivided. It will be noticed that a progressive decline (towards the rogues) can be often seen in the offspring of *branches* as well as on the main stems.

In Table II the plants are classified in the five classes which we have arbitrarily used. Class 1 is the true type; Class 2 differs from it slightly and evasively in foliage, but chiefly in having some curvature in the pods; Class 3 are the pointed intermediates of the kind which show the gradational changes; Class 4 contains plants below Class 3 and approaching Class 5, which last are the genuine rogues. Of these classes, 1 and 2 are non-pointed; 3, 4, and 5 are pointed. There is a complete series of intergrades, both in somatic appearance, and in genetic constitution as indicated by the families produced.

For Table II we have chosen those families which contained at least one non-pointed plant. The progressive decline towards rogues affects the lower classes, and not merely the frequency of the non-pointed plants. The same feature is also shown by the families containing only pointed plants, which we have not included in this epitome. It appears also in the distribution of the several pointed classes resulting from crossing the intermediates as female with type, the pointed plants thus produced by the *lower* pods being chiefly Classes 3 and 4, the corresponding plants from the upper pods being chiefly rogues of Class 5. This feature, which is not shown in Table I, was most conspicuous when the tall intermediates were used.

Inasmuch as the relative proportions of the several kinds of offspring produced by Class 3 plants (and doubtless by Class 4 also)

a few of these ought, no doubt, to have been included as genetically comparable. The figures given for the results of self-fertilisation are not all derived from the plants actually used for the crosses, but include any results from flowers of known position borne by comparable plants.

TABLE II. *Families produced by Pointed Intermediate Plants (self-fertilised) which gave a small minority of non-pointed members. Results tabulated according to the flowering nodes from which the seeds were taken.*

Register no. of parent	Ordinal no. of flowers	Classes: Non-pointed 1	Non-pointed 2	Pointed 3	Pointed 4	Pointed 5
$36^1/6$ Main stem	1–7	—	1	—	—	28
	8–11	—	—	—	—	27
	12–17	—	—	—	—	28
Branch from 7th node	1–5	—	6	1	2	22
	6–8	—	1	—	—	20
	9–15	—	—	—	—	39
$41^3/6$ Main stem	1–4	—	5	5	—	9
	5–8	—	1	—	—	13
	9–12	—	—	—	—	16
	13–15	—	—	—	—	16
Branch from 9th node	1–3	—	—	6	—	8
	4–6	—	—	—	—	17
	7–9	—	—	—	—	22
$178^4/6$	1–4	—	1	—	3	12
	5–9	—	1	3	—	21
	10–14	—	—	—	—	25
$178^7/6$ Main stem	1–4	—	4	—	—	16
	5–8	—	—	—	—	22
	9–15	—	—	—	—	26
Branch from 8th node	1–7	—	4	2	—	33
	8–11	—	—	—	—	15
$192^1/6$	1–6	—	4	2	—	11
	7–9	—	—	—	—	22
	10–14	—	—	—	—	21
	15–19	—	—	—	—	24
$205^3/6$	1–5	1	1	—	3	18
	6–9	1	2	2	—	23
	10–15	—	—	2	—	35
$258^1/6$ Main stem	1–8	—	1	3	—	31
	9–13	—	—	—	—	28
	14–21	—	—	—	1	35
Branch from 8th node	1–2	1	3	—	—	8
	3–7	—	—	1	1	36
$349^2/6$	1–7	3	4	7	—	11
	8–13	—	—	—	—	33
	14–15	—	—	—	—	10
$278^1/6$	1–5	—	7	8	—	11
	6–9	—	—	6	—	25
	10–16	—	—	1	2	11

TABLE II (*continued*)

Register no. of parent	Ordinal no. of flowers	Classes: Non-pointed 1	Non-pointed 2	Pointed 3	Pointed 4	Pointed 5
$25^6/7$	1–2	2	—	2	—	6
	3–5	—	—	—	—	15
	6–7	—	—	—	—	17
$112^1/17$	1–2	3	3	1	1	1
	3–4	—	3	—	4	1
	5–6	—	—	—	—	9
	7–8	—	—	—	—	3
$183^1/7$	1–2	—	1	—	—	14
	3–4	—	—	—	1	12
	5–7	—	—	—	—	16
$185^5/7$	1–2	2	4	2	—	1
	3–6	1	3	10	5	9
	7–8	—	1	3	3	3
	9	—	—	—	1	3
$265^1/7$	1–3	—	5	—	2	7
	4–5	—	—	—	1	7
	6–7	—	—	—	—	8
$453^1/7$	1–2	—	2	3	1	3
	3–4	—	—	1	1	7
	5–7	—	—	—	—	9
$457^1/7$	1–2	—	1	—	—	9
	3–4	—	—	—	—	11
	5–6	—	—	—	—	5
	7–8	—	—	—	—	12
	9–11	—	—	—	—	5
$254^1/8$	1	—	—	—	1	6
	2–3	—	1	1	1	8
	4	—	—	—	1	8
	5–6	—	—	—	1	15
	7–10	—	—	—	1	22
$373^4/8$	1	—	1	1	1	1
	3–4	—	—	—	—	9
	5–6	—	—	—	—	14
	7–8	—	—	—	—	11
$556^1/8$	1–3	1	4	1	2	12
	4–5	—	1	1	4	7
	6–8	—	—	2	2	10
$603^1/8$	1	—	—	—	—	7
	2–4	—	1	—	—	13
	5–8	—	—	—	—	19
$621^9/8$	1–2	—	1	—	—	13
	3–4	—	—	—	—	13
	5–9	—	—	—	1	22

depend on the absolute height of the parents, it is impossible to give any significant figure for these proportions, but the averages produced by the self-fertilisation of the several classes are roughly as follows:

	Non-pointed	Pointed
Class 1	47	1
,, 2[1]	12	1
,, 3	1	10–20
,, 4	1	160
,, 5	0	All rogues

Since plants can be found giving every proportion of non-pointed to pointed, the actual ratios observed in any group of plants mean little unless the group can be accurately defined. Such definition of somatic characters is not strictly possible. In choosing plants for crossing, we took those which, judged on their *early stages*, might be expected to throw a small minority of non-pointed plants, for our object was to examine the gradational effect, which can only be manifested by plants of that composition. In Table II, however, we have plants chosen when ripening, on their *adult* characters, selected further on account of their being well grown, and the result is that these, as tested by their offspring, proved to be of a somewhat higher constitution than those chosen for crossing. For any plants which did eventually show the rogue "points" are not too high to show the gradational effect, though judged as young plants, before they had assumed the points, they would not have been known to be available for the purposes for which the crosses were made. The higher the level at which the points appear, on the whole, the higher is the proportion of non-pointed plants found among the offspring, but this correspondence is rough, and only becomes apparent when long series of families are examined.

Recapitulation

The three chief phenomena may be recapitulated:

1. Reciprocal crosses between type and rogue give plants which, as they develop, turn into rogues.

2. Though the characters of the type are certainly introduced, manifesting their presence by affecting the form of the young F_1

[1] Class 2 in our first paper [this volume, p. 243] was not the exact equivalent of that subsequently adopted. We had not then appreciated that the points are the best criterion, and we previously included in Class 3 plants which we now know to belong genetically rather with Class 2. The inclusion of such plants in Class 2, of course, lowers the average offspring of that class.

plant, they very rarely[1] take part in the germ lineage, being apparently left behind in the lower nodes.

3. Plants really intermediate between type and rogue nevertheless *exist, but never breed even approximately true. Their germ cells may* be either type, intermediate (of at least two kinds), or rogue. The proportion of gametes carrying type-characters is different on the male and female sides. In both sexes the ratio shows gradational change.

Of the egg cells of the lower flowers, up to about the 10th flowering node, rather more than 50 per cent. carry the type-characters—or, at least, the non-pointed character—above which level the proportion declines.

Of the pollen in the lowest two flowers, only about 20 per cent. is type-bearing, and the proportion diminishes rapidly in each successive flower above this level.

Discussion

Features somewhat comparable with the first two of these peculiarities have been recorded, but the third is, so far as we are aware, as yet without parallel. Biffen[2] has observed the total "suppression" of a character, grey chaff, introduced by Rivet wheat, in a cross with Polish; and, in variegated *Capsicum*, crossed with green, Ikeno[3] never recovered the green in later generations. Baur[4] interpreted certain wholly white and wholly green offspring obtained in crosses between white-skinned and green plants by the very probable suggestion that the green or white characters might have been omitted by somatic segregation, though the inference was scarcely capable of direct proof. Winge[5] also saw something possibly analogous in *Humulus*, traces of variegation appearing in lower leaves of plants, which subsequently became green. None of these examples, however, are strictly comparable, but Winge's case perhaps comes nearest.

A *gradational* change in the numerical proportions of the gametes at the successive nodes has not, we believe, been elsewhere observed. The distribution of the type gametes borne by the pointed inter-

[1] The exceptions mentioned in our first paper [this volume, p. 252] should probably be thus interpreted. A few others have since been met with which hereafter will need detailed description.

[2] *Journ. Gen.* v, 1916, p. 227.

[3] *Ibid.* vi, 1917, p. 201.

[4] Especially *Zeits. f. ind. Abstammungslehre*, iv, 1910, Heft 2.

[5] *C.R. Lab. Carlsberg*, xiv, 1919, No. 3, p. 11.

mediates corresponds, no doubt, in a loose way with the distribution of vegetative vigour. But weak growth on type plants is not specially likely to bear rogues, nor do rogues, however luxuriantly growing, produce types. Aetiological interpretations of this kind are inconsistent with all that we have learnt of genetic principle. Nevertheless, the coincidence may not be without significance.

Where the output of the several sorts of gametes is so uncertain no gametic system of a Mendelian kind can be propounded. The most that can be expected of such a system in this case is that it should qualitatively represent the distinction between the genetic nature of the classes here called 2 and 3. Since type (T) and rogue (R) gives F_1 rogue, neither of these intermediates can receive a rogue gamete in fertilisation. Since also these two classes differ from the type, the gametes composing either of them cannot *both* be type-bearing. From this reasoning it appears to be practically certain that two sorts of intermediate gametes must exist, the one more type-like, T', the other more rogue-like, R'. TT' will then represent Class 2 and TR' Class 3; but where, as in this case, there is no clear discontinuity no analysis can be pressed. All that can be positively stated is that there are two sorts of intermediate gametes, that both are unstable, being incapable of constituting a stable zygote, and that when united in *fertilisation with a type gamete, the resulting zygote is nearer the* type than any combination of intermediate gametes would be.

Class 2 plants throw perceptibly more pointed plants than do the real types (see p. 305) but they do not show the gradational phenomenon as Class 3 plants do. Evidently the gradual extrusion of the type at the successive nodes must be a process similar to that by which the type is extruded in the base of F_1, differing only in that it is prolonged over a longer series of nodes. The actual data suggest that the gradational phenomenon occurs with greatest intensity in the more rogue-like of the intermediate plants and is less well marked in those which, judged by their offspring, are higher (more type-like) in genetic composition, being absent altogether in Class 2. Discussion of these points cannot be given in brief.

As it seemed possible that the types might be tetraploid, counts of chromosomes were made by Miss Nesta Thomas, but the number found in both rogue and type was the same (seven for the haploid number)[1].

The persistent recurrence of rogues among the offspring of types

[1] Since confirmed by Professor K. Matsui.

must indicate some liability to an error in cell-division. Once the abnormality has occurred, of which pointed leaflets are the ostensible indication, there is a progressive change in successive generations such that, assuming equal fecundity in all classes, the progeny would in a few generations consist of rogues in overwhelming proportions. It was a commonplace of practical breeders and of conventional evolutionists that when selection is suspended, a breed "degenerates." This doctrine, promulgated, as it commonly was, without any reservation as to crossing or reference to critical purity of line is fallacious as an expression of physiological truths however much the objective consequences may seem to fulfil the prophecy. In the present example the popular conception of degeneration is precisely realised. So far as we know it unique.

GENETIC SEGREGATION

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THE later developments of Mendelian analysis have been in the main an attempt to elucidate the scope and nature of Segregation. Mendel proved the existence of characters determined by integral or unit factors. Their integrity is maintained by segregation, the capacity, namely, to separate unimpaired after combination with their opposites. Our first aim has been to discover specifically what characters behave in this way, whether there is any limit to the scope of segregation, or any characters or classes of characters which are determined by elements unable to segregate simply. The second object has been to decide the time and place in the various life-cycles at which segregation occurs. It is with the latter problem that I propose to deal more particularly in this Lecture, but a brief consideration of the range of characters, subject to segregation, is appropriate.

1. *The Scope of Segregation*

Of the classes of features by which animals and plants are distinguished, most have now been shown to be dependent on segregable elements. It is perhaps noticeable that we have no quite clear proof that the factors governing differences in number, meristic characters in the strict sense, commonly behave so simply as those determining other characteristics. There are examples of parts repeated in series, such as the extra toe of the fowl (a dominant) and the leaf of the monophyllous Strawberry with a single leaflet (a recessive) which have a factorial inheritance, but the resulting terms, especially the heterozygotes, are indefinite. In the polydactylous fowl, for example, the heterozygote has a great variety of shapes. The hind toe is most often represented by two sub-equal digits, but the duplicity may be so slight as to appear externally only as a division of the nail. It may also assume another very different form, in which there is only a single many-jointed digit representing the usual pair. In the monophyllous Strawberry the homozygous recessive, whether before or after immediate extraction from the heterozygote, shows fluctuations to a 2- or 3-leaved condition[1]. Such fluctuations are common among forms distinguished by meristic peculiarities. There is not the uni-

[1] Richardson, C. W., *Journ. Gen.* III, 1914, p. 171.

NOTE.

formity and simplicity which is such a striking feature of variations in colour and many other substantive characteristics. The evidence as to meristic differences is however still scanty, and it is too soon to decide what importance should be attached to this preliminary impression.

With more confidence we recognise that merely quantitative differences seldom, if ever, have a perfectly simple inheritance. There are two obvious interpretations: (1) that the factors do not usually segregate clean; (2) that the number of factors involved is so large that their effects are masked. Adequate discussion of these two possibilities could only be given at considerable length. On the whole, I incline to the former alternative, but the material for a decision scarcely exists as yet. Certain examples should be noticed in which, though the most obvious differentiating feature is quantitative, the underlying physiological distinction is more probably to be referred to a qualitative factor. Height in certain plants is a good illustration. It is ostensibly a quantitative feature, and the talls segregate clean from the dwarfs. But in various cases, *e.g.* Peas and Sweet Peas, the dwarfs are also a darker green. The dwarf of *Campanula persicifolia*, especially (about 8 inches high), is a plant so strikingly different from the type (2–3 feet high), that it is sold as a species *C. nitida*. The leaves of the dwarf are an intense, dark green[1]. This variety is, of course, a recessive and segregates without intermediates, yet, if the qualitative distinctions were less evident it might easily be classed as a variety in quantity. But the critical distinction is certainly qualitative and the great difference in size is consequential. Though in such cases segregation is complete, it may almost be said to be characteristic of purely quantitative distinctions that one or other of the original parental types fails to reappear in its extreme form after a cross. So usual is this feature in quantitative segregation that the phenomenon must have special significance.

Another fact is beginning to emerge which must contribute to the shaping of a conception of the physiological nature of segregation. We have learnt that groups or complexes of factors may segregate whole. To such a complex the distinction in sex is due, but in certain cases it may break up. The occurrence of a large spur in fertile hens (Leghorns, for instance) must be regarded as due to the absence of that part of the sex-complex which in the normal hen inhibits the

[1] The ovary projects in a curious way above the sepals so much, that were the plant not a *Campanula*, botanists would describe this ovary as superior.

growth of the spur. In ordinary fowls the whole inhibiting group remains on the female side, but the spur-inhibiting element can evidently separate from the rest. On the other hand, when in the cocks of certain breeds (as occasionally in Wyandottes) there is no spur, we may perhaps conjecture that this element has been transferred to the male side[1].

The presence of the characteristically masculine comb and wattles in the male Sebright, which is otherwise henny, shows that another factor similarly detachable governs their development.

To the breaking up of large compound factors the production of intermediate types, such as occur among the colour-varieties of plants, is in all likelihood due. The Sweet Pea and the Snapdragon have now an innumerable series of such colour-forms which may be represented as having arisen by the disintegration of the various anthocyanins. That, at least, is the simplest way in which their origin can be conceived.

To the final result many qualifying elements contribute, and these may naturally be separate entities. But change in the amount of the same colouring material, and diminution in the mere extent of its distribution, are common features of these graduated series. As the cultural development of the species progresses, more and more of these quantitative intermediates appear, and are selected, until a practically continuous series is produced. Although the inter-relations of the whole series can be represented by a factorial scheme, the assumption that each of these factors had an aboriginal individuality appears gratuitous. In *Antirrhinum*, for instance, the ordinary self-coloured flower segregates as a single unit from the white. But there are "Delila" forms having the "face" coloured and the "throat" white. Another variety has the "lip" coloured and the peripheral parts white, and to this again there is an almost exact counterpart in which the peripheral areas are coloured and the lip nearly white, and between these again there are further intergrades. Apart from factors modifying its quality, the colour of the whole corolla, segregating as a single entity from the white, would without hesitation be represented as

[1] *After much experiment the genetics of spur-development are still very obscure. In the course of a long series begun by crossing spurred Leghorn hens with a spurless* Wyandotte cock (giving F_1 normal in both sexes), neither form has reappeared in F_2 with its original development. Very rarely a hen with minute spurs has appeared, and occasionally a cock with the spurs sensibly reduced. Nor from spurred hens × F_1 ♂ has anything approaching the original types been raised. Conceivably the detached element is able to join again with the rest of the female complex.

depending on a single factor. Subsequent experience that this entity can break up into an indefinite number of fractions is not evidence that the original representation was wrong. This reasoning applies to a great range of phenomena.

In view of the chromosome theory of linkage, it is therefore worth remarking that we do not find linkage especially frequent among these fractional factors. Have they, then, been distributed among different chromosomes? If in *Antirrhinum*, the colour of the face and of the throat were lately parts of a single factor for the total flower-colour, would not linkage between them be expected? Nevertheless, in cases of this sort, so far as I know, linkages have not been found with any special frequency.

The segregation of a group of differences—and presumably factors—in combination has lately been shown by Renner[1] to occur with extraordinary frequency in the Œnotheras, and this peculiarity is without doubt at the bottom of the difficulties which have beset the genetic analysis of these plants. The complexes are in several forms or species not borne equally by the two sexes of the same plant, and most of them are unable to exist in the homozygous state. These discoveries greatly elucidate the Œnothera problem. For instance, not only *Œn. lamarckiana*, but *biennis*, *muricata*, and others also, are not homozygous types, but heterozygotes of a special kind. Consequently, the production by them of "mutants" is not capable of the simple interpretation originally applied to them by de Vries. Renner suggests that the mutants arise owing to some interchange between the complexes which at present we cannot investigate, but whatever be the exact manner of their origin we cannot regard them as genuine examples of the production of novel forms by a homozygous type.

Before leaving this part of the subject, we may notice that the supposition that segregation is concerned solely with characters of a superficial or trivial nature has been long ago disproved. Baur's Antirrhinums, the study of which was continued by Lotsy, were an excellent demonstration to the contrary, for they provided many illustrations of segregation in features, the "specific value" of which no systematist would question. If further evidence were needed, it may be found in the fine series of experiments lately published by Heribert-Nilsson[2] in *Salix*, which, contrary to the belief long ago

[1] *Zts. f. ind. Abstammungs- und Vererbungslehre*, XVIII, 1917, p. 121.
[2] *Lunds Universitets Årsskrift*, N.F. Avd. 2, XIV, 28 November, 1918.

entertained by Wichura, show that, when F_2 families are raised in adequate numbers, very striking segregation occurs in the species-crosses. Many geneticists are inclined to the view that segregable characters should be pictured as implanted on an irreducible base which is outside the scope of segregation, but no means have yet been devised for testing the reality of this conception.

2. *The Moment of Segregation*

The next question is to determine when in the various life-cycles segregation can occur. Obviously it is a phenomenon of cell-division. If we knew nothing of the genetics of plants we might confidently adopt the view which Morgan has so successfully developed, that normal segregation and redistribution happen exclusively in the process of reduction. Though unconvinced, I cannot deny that linkage and crossing-over may well be represented provisionally, as effected during synapsis. The scheme previously offered by Punnett and myself as a diagrammatic plan capable of representing these phenomena is certainly far less attractive. There is evidence that in certain plants, *e.g. Matthiola*, the composition of the families derived from single pods shows very great and perhaps irregular fluctuations, and the normal ratios for those families is only found by taking the average of many, but no sufficient statistical examination of such cases has yet been made. In some suitable case estimations of the offspring derived from individual anthers might be of value in this connection. Renner, by examining the starches of the pollen grains in Œnotheras, has lately made visible that di-morphism, of which we had previously genetic proof, and perhaps this novel and striking observation might be used for the purpose of mapping the distribution of such a character among the pollen grains. Meanwhile, it must be granted that no indication that gametic linkage results from somatic differentiation has yet been obtained.

When, however, we examine the view that linkage of factors is a consequence of their association in a chromosome, we must observe that there is no body of evidence that the number of linkage systems agrees with that of the chromosomes, a primary postulate of Morgan's theory. *Drosophila* is the only example which has been adequately investigated. The cytological appearances are not readily consistent with the other postulate of Morgan's case, that crossing-over is effected by anastomosis of chromosomes and exchange of materials between them. In our present ignorance of the physical nature of

the factors we are not obliged to assume that an actual transference of material is an essential condition for an exchange of properties; but since Morgan's suggestion is made in that form we are bound to notice how difficult it is to interpret the visible phenomena of cytology in accordance with that hypothesis. Without personal familiarity with cytology no one can have a confident opinion. I observe, however, that in his most recent publication on these subjects, E. B. Wilson[1] gives a very emphatic "counsel of caution," remarking that writers on genetics have taken too much for granted, and that for the present the genetic development of the chromosome theory has far outrun the cytological. To a layman the visible appearance of chromosomes is scarcely suggestive of the prodigious material heterogeneity demanded, and the general course of cytological evidence seems to indicate that the *rôle* of the chromosomes is passive rather than active. Though showing features of regularity, they are capable of very wide variations without transgressing the limits of viability, which could scarcely be the case were every detail in their organisation critical. The appearance of chromosomes is not to me suggestive of strings of beads of extreme heterogeneity, but rather of strands of some more or less homogeneous substance; and in so far as numerical and geometrical order is exhibited by them, it would, in my opinion, be more proper to compare this regularity with that seen, for example, in drying mud or in the formation of prisms of basalt than to attribute to it a more fundamental meaning.

Leaving these speculative considerations, and limiting our inquiry to the concrete question, at what moment in the cycle does genetic segregation occur, we reach a perfectly definite answer: that whatever future research may decide as to the occurrence of segregation in animals—which, for aught we know, may always be effected at the reduction-division—there is no such limitation in plants. We are now thoroughly familiar with a large group of examples in which the genetic properties of the male and female cells of the same plant are quite different. In these, at all events, the reduction-division cannot be the moment of the segregation by which these characters are distributed.

The first case detected was in *Matthiola*, where Miss Saunders' results proved that in the double-throwing singles the pollen carries exclusively doubleness, the eggs being mixed, some single and some double. A similar condition was shown to exist in regard to the cream

[1] *Amer. Nat.*, May–June, 1920, p. 210.

and white plastids respectively, the pollen grains bearing exclusively cream. De Vries observed a comparable arrangement among the Œnotheras, and Renner has lately shown that the phenomenon is widely spread in that group, thereby providing a consistent interpretation of much that was formerly obscure in the genetic behaviour of these plants. In *Campanula carpatica* Miss Pellew proved that the pollen grains of the hermaphrodite form called *pelviformis* carry exclusively femaleness, and preponderantly white flower-colour (the plant being heterozygous for blue). The case of Petunia investigated by Miss Saunders[1] is somewhat peculiar in the fact that in the heterozygous singles the male side carries the dominant singleness only, since in those instances to which the conception of dominance can be applied, it is the male which commonly carries the recessive. Segregation of these characters cannot in plants so organised be supposed to take place later than the constitution of the male and female organs, and therefore the reduction-division cannot be the one critical moment. The suggestion has been made that germ cells of the missing kinds may be in reality formed and perish before reaching a functional stage. As regards tbe Œnotheras, where shrivelled pollen grains abound, this conjecture is very plausible and probably correct; but when as in the other cases here quoted, the pollen grains are uniformly sound, the hypothesis is inapplicable and without evidential support. Moreover, even if it were true that certain classes of germ cells perish in one or other of the sexes, that would hardly alleviate the difficulty, for this differential viability would remain to be accounted for, being itself a phenomenon of segregation.

Begonia Davisii[2] is another curious illustration in which segregation must occur even earlier. This plant is a wild, true-breeding species, with ordinary single flowers. All the pollen grains however carry doubleness, and used on the female flowers of doubles give offspring all double (single being the dominant). The pollen of this plant is as uniform and perfect as those of any species I have ever seen. We must therefore conclude that the segregation by which singleness separates from doubleness is effected not later than the formation of the rudiments of the male and female flowers. Cytological investigation may no doubt show that the distinctions between the genetic properties of the male and female are associated with visible nuclear differences, but I see no reason for anticipating that such differences must exist.

[1] *Journ. Gen.* I, 1910, p. 57.
[2] [This volume, p. 289.]

Cells which differ in their genetic potentialities must of course differ in physical constitution, but there is no reason to suppose that this difference need be in any way dependent on chromosome structure.

As regards *Campanula carpatica* "*pelviformis*" and *Begonia Davisii* experiment has shown that the peculiar kind of segregation which they exhibit may recur in their offspring. In the *Begonia*, if the female of *Davisii* be fertilised with pollen of an ordinary double tuberous *Begonia*, the doubleness so introduced stays on the male side just as the doubleness of its own male does, and a plant so bred has its pollen all double. But if the male of *Davisii* be used on the female of an ordinary single, there is no restriction of doubleness to either sex of the offspring. The peculiarity of *Davisii* must therefore be attributed to the special properties of its female side. The *Campanula* case is complex and has not yet been fully explored, but at least from the female side of *pelviformis* plants have been raised which retain the properties of the mother as regards the distribution of the white and blue colours.

We have at the John Innes Institution been lately investigating a similar case in flax, which though comparable has some special features. A dwarf flax (*Linum usitatissimum*) of unknown origin, presumably a stray seedling of one of the varieties grown for oil, was fertilised with pollen from our tall fibre strain. Both parents breed true to the fully hermaphrodite condition with anthers perfectly formed, and the F_1 plants were normal in this respect. F_2 consisted of hermaphrodites, and a recessive form with aborted anthers, generally contabescent and not dehiscing at all, but having occasionally a few grains of good pollen. The ratio was a normal 3 : 1. The recessive, having occasional grains of pollen, self-fertilised, gave similar plants with anthers wholly or almost wholly aborted. The normal F_2 hermaphrodites gave in F_3 families which showed that some of the F_2 plants were pure normals, others heterozygous in the ordinary way. But when the recessives were fertilised with pollen from three several varieties of tall fibre flax, only recessives were produced. These tall flaxes therefore are normally heterozygous for the recessive or "sub-female" condition, and this in segregation is permanently relegated to the male side of the plant, while the female side takes the hermaphrodite factor. Segregation in regard to the same recessive may take place in one of two ways. It may be *unilateral*, as it is when in heterozygous association with the female of the tall flaxes, or it may be *ambilateral* and unrestricted to either sex

when it is in association with the female of the oil flax. We must infer that the female halves of the two types differ in some critical respect which decides the manner of the segregation.

Unilaterality may also show itself as a difference in the closeness of linkage on the two sex-sides of the same plant, and no doubt this fact may have a bearing on the interpretation of the foregoing cases. The late R. P. Gregory discovered the first case of this, in *Primula sinensis*. He found that the linkage between magenta colour and short style was closer in the eggs than in the pollen. Recent work on a larger scale has given 10·9 : 1 as the female linkage and 6·4 : 1 for the pollen. A similar difference has been also found for the linkage between green stigma and "reddish" stem (as opposed to dark red), the value being 29·8 : 1 for the eggs and 41·7 : 1 for the pollen. In both examples, individual families show wide fluctuations, and these values should for the present be regarded as approximate only. Whatever be their meaning, they show that some segregation has occurred in the formation of the two sets of sexual organs, such that the process of gametic differentiation is not the same in both.

Besides these examples of differentiation between the male and female sides, there are others proving that segregation may occur at other stages in somatic development. The most obvious examples are the variegated plants. I have discussed this subject elsewhere in connection with reversible periclinal "chimæras" of white over green which produce shoots having the white enclosed in the green[1]. To these must now be added the cases in which the plants arising from adventitious buds differ from the plants which produce them. I have described one of these examples in *Bouvardia*. The pinkish white "Bridesmaid" gives the red-flowered "Hogarth" from its root-cuttings. Three similar occurrences have been found in fancy Pelargoniums. The root-cuttings of a white-flowered variety, "Pearl," gives a red-flowered form, very like "Mme Thibaut." "Mrs Gordon," which is a full rose-pink, with whitish edges, gives from its root-cuttings flowers in which the two posterior petals are marked with dark red, not unlike the variety "Cardiff." A more striking case is that of "Escot," which gives from its roots plants with bright pinkish red marks, those of the original being purplish red. The most curious feature of this case lies in the increased size both of the plant and the flowers coming from the roots, and it is scarcely possible to see the petals of "Escot," which are characteristically rolled back,

[1] [This volume, p. 282.]

side by side with those of the root-form, which are not only larger but also flat, without surmising that this rolling back is an expression of the greater size of the larger petal contained within the smaller, causing a want of correlation between the growth of the inner and outer tissues.

Buckling or crumpling of leaves through want of correlation was a conspicuous feature of some of Winkler's "graft-hybrids," made from *Solanum nigrum* and *S. lycopersicum*, when the larger tomato was enclosed within the smaller species. We have had a precisely similar example in a salmon-fringed Pelargonium bred by Mr Jarman of Chard. The leaves are obviously buckled, the petals are laciniated, and the female parts aborted, though the anthers are perfect. This male and deformed flower is proper to the outer tissues only; for on two occasions the plants have produced shoots with large flat leaves and normal hermaphrodite flowers with their petals entire. Obviously, this normal plant was enclosed within a skin of the fringed type.

In all these examples, a somatic segregation has occurred which determines the genetic potentialities. The interpretation that they are *periclinal* chimæras is probably correct for the most part. The fringed Pelargonium is obviously of this nature. Nevertheless, the fact that a root-cutting consistently produces a certain type of plant which is not the original does not prove that the distribution is periclinal. Another possibility is well illustrated by the case of a variegated *Spiræa ulmifolia*, having the stem, petioles, and (basal) centres of the leaves without chlorophyll[1]. The growing point has the power of laying down green tissue in the lateral areas only, the internodal regions being albinotic. Root-cuttings from this form give albino plants which die after the development of two or three small leaves. Now in this case we can see the distribution of the green and white respectively, and we recognise that the roots give albino plants because they belong wholly to the albinotic area. On similar lines it is possible to interpret the *Bouvardia* and other cases. The distribution of the two types in the same plant may be such that one is limited to the root and internodes, while the other is in the nodal structures.

That considerations of this kind are not fantastical is proved by

[1] This is somewhat like the Pelargonium named by Messrs Cannell "Freak of Nature," in which the chlorophyll has a closely similar distribution, and it, like the *Spiræa*, is sterile on both male and female sides. In this *Spiræa* I have never seen pollen, but very rarely a fruit is formed, which, no doubt, is due to an occasional development of a bud in the green area, an occurrence frequent in variegated plants. Whether these fruits contain viable seeds is not yet known.

the genetical phenomena seen in the case of "rogues" in culinary peas, which Miss Pellew and I have been investigating for a number of years[1]. The rogue is a peculiar, wild-looking plant, differing in various ways from the type, chiefly in having pointed leaflets. Crosses between it and the type give plants which in their lower parts are intermediate, though turning into rogues as they develop. The self-fertilised offspring of rogues and also of these F_1 plants are always rogues, and evidently the type-characters introduced from the type-parent are left behind in the lower parts. Such a case may perhaps be compared with the condition seen in the variegated *Spiræa*, and we may fairly conjecture that if it were possible to raise root-cuttings from the F_1 peas, they would produce types.

A more gradual exclusion of the type-elements in the lower parts is seen in certain intermediates. These may scarcely differ from types in the lower parts, though changing to rogues, sometimes abruptly, sometimes gradually, as the series of flowering nodes is developed. Reciprocal crosses between the successive flowers of such plants and the flowers of types has shown that, together with the gradational change in the somatic structures, there is also a gradational change in the proportion of gametes bearing the rogue and type-characters respectively. This proportion and the rapidity of the change differ on the male and female sides. Of the *egg cells* in the lower flowers, up to about the 10th flowering node, rather more than 50 per cent. carry the type-characters—or at least the non-pointed leaflets—but above this level the proportion of types declines. Of the *pollen* in the lowest two flowers only about 20 per cent. is type-bearing and the proportion diminishes rapidly in each successive flower above that level.

In all the examples given hitherto the segregation is in diploid tissues, but a comparable phenomenon has been proved by Collins to occur in the *haploid* axis of a moss (*Funaria*). In a diœcious moss, as the Marchals have shown, sex segregation occurs at spore-formation, the division in which reduction is effected. This, of course, agrees with cytological expectation, though so far as I know, the details have not been observed. But from the leaves of mosses placed in nutrient fluids new plants may be raised without great difficulty, and Collins found that the (perigonial) leaves surrounding the male organ thus propagated, produce *exclusively male* axes[2]. He has since raised similar cultures from the (perichætial) leaves surrounding the female organ, and, as related in the paper following this, from them

[1] [This volume, p. 298.] [2] *Journ. Gen.* VIII, 1918–19, p. 145.

monœcious plants resulted. The proof is thus complete that in a haploid tissue a segregation of sex can occur.

The inference may be drawn that the factors for other characters may similarly be liable to segregate in the haploid state. In this connection I may mention a case which though as yet obscure, perhaps fulfils this expectation. In botanic gardens a variegated maiden-hair fern (*Adiantum capillus-Veneris*) is grown which has wedges of white tissue irregularly distributed in the segments. This plant produces spores freely[1], and these give rise to prothallia which in several cultures raised here have always been entirely green. But when ferns arise from these green prothallia by the sexual process, they are of three kinds, green, white or variegated like the parent plants. The fact that the prothallia should be all green is entirely unexpected and creates a distinct problem, but it is evident that segregation must occur either in some of the cell-divisions by which the prothallia proliferate, or in those by which the gametes are formed, in either case in haploid tissue. This segregation is essentially different from that by which the differentiation of organs, such as the archegonia and antheridia, is accomplished, inasmuch as it relates to elements determining the characters of the next generation.

From the evidence given it is clear that in a wide view of living things segregation cannot be exclusively a property of the reduction-division, and for the present, it should be regarded as a possibility which may occur at any division in the life-cycle.

[1] I have not satisfied myself that spores are produced in sori on the white areas.

ROOT-CUTTINGS AND CHIMÆRAS. II

(With Plates XIV, XV)

[*Journal of Genetics*, XI, 1921]

Bouvardia.

IN a former paper[1] I recorded the production of the red-flowered variety Hogarth from the roots of *Bouvardia* Bridesmaid which has pinkish white flowers. This behaviour is perfectly consistent. At various times we have raised from Bridesmaid 29 root-cuttings (besides others not counted), which in every case bore Hogarth flowers. Very rarely a streak or flake of pinkish white has occurred on these flowers such as I have seen on other varieties of *Bouvardia* (*e.g.* Cleveland and Lemoinei) but they are exceptional. Perhaps one or two such flakes are seen in a season among our collection, and they do not come with any special frequency on the derived Hogarths.

From Hogarth *ex* Bridesmaid's roots 64 root-cuttings have been raised, all Hogarth *except one which was Hogarth colour but single-flowered*, whereas Hogarth and Bridesmaid are fully double. This single had anthers which dehisced containing much pollen, in microscopical appearance all bad. Singles arising as root-cuttings from double Bouvardias have often been recorded in literature, especially from Alfred Neuner, but this is the only instance observed here. A. Neuner has only given us three root-cuttings which have flowered as yet, both double, exactly like the parent plant.

From Hogarth *ex* Hogarth *ex* Bridesmaid 63 normal Hogarth have been raised as root-cuttings and from these again have come 13 normals.

From the *single* Hogarth (*ex* H. *ex* B.) we have raised 6, all singles like the immediate parent.

The following kinds have given root-cuttings which on flowering were exactly like the parent:

A. Neuner, white double (3).
elegans, scarlet single (15).
Humboldtii, white single, glabrous (23).
jasminiflora, whitish pink (1).
King of Scarlets, scarlet single (12); and from these again (7).
Lemoinei, red double (25).
Pres. Garfield, pinkish white double (2).

[1] [This volume, p. 264.]

Priory Beauty, rose single (3).
The Bride, white single (2).
Vreelandii, white single (10).
leiantha, a species, scarlet single (9).
and from a seedling, scarlet single, produced by the late Mr Allard from Cleveland × *leiantha* (2).

Vulcan, a scarlet single, short-styled, gave 27 root-cuttings like itself and *one rose-pink single*[1].

President Cleveland, scarlet single, long-styled, gave 23 true to type, and 8 peculiar, having flowers scarlet marbled with white. These flowers were rather smaller and looked unhealthy, but for several seasons they have kept the same character, and the plants seemed in normal health. The margins of the petals are scarlet, and the marbling consists of whitish lines irregularly distributed over the petals, coalescing towards the central and basal parts. In the streaks the substance of the petals is somewhat thinned, a feature which gives them a depauperated appearance. Our stock of Cleveland came from two commercial sources, and the two lots were not kept distinct. It is therefore doubtful whether both kinds of root-cuttings came from one plant in this case.

From roots of true Cleveland *ex* Cleveland 21 were raised all true; and from them again 7 all true.

From roots of marbled root-cuttings of Cleveland we had 16 marbled, 11 with slight and irregular traces of the marbling, and one *not* marbled, being true Cleveland.

A variegated form of Humboldtii, having a green core and a pale yellowish green cortex, gave 2 root-cuttings green, as might be expected. These have not yet flowered.

In style-length the root-cuttings have always agreed with the parent plant, shorts coming from shorts and longs from longs.

Pelargoniums (Fancy).

Fancy and especially "Regal" (*i.e.* semi-doubles with petals crumpled) Pelargoniums have been said to give root-cuttings with flowers differing from those of the parent plant. This has been observed in three cases.

Escot (Pl. XIV, fig. 1) has flowers white with a large purplish red blotch on each petal. It is characteristic of the variety that the petals,

[1] Though this "sport" came alone there is no reason to doubt that its origin was correctly recorded. We had no similar variety.

especially the two dorsals, roll back more or less. A plant gave off a natural "sucker" (from a root) which bore flowers as shown in Pl. XIV, fig. 2. They are larger than type (70 mm. across the largest flower against 62 mm. in the parent); and flat, showing no disposition to roll back. The peripheral areas of the petals are pinkish, not white, and the blotches much redder than those of type, a feature insufficiently rendered in the coloured figure as reproduced. A root-cutting has since been raised from Escot, and its flowers agree with those of this sucker. The rolling-back of the petals in the parent is perhaps due to strain produced by the greater size of the flower proper to the included "core." The root-cuttings are somewhat taller than the type.

Mrs Gordon has flowers white and pink as shown in Pl. XIV, fig. 3, with guide-marks of the dorsal petals only lightly represented. Three root-cuttings are all alike (Pl. XIV, fig. 4), have much more colour, a full pink, on all petals, and in addition deep crimson guide-marks. These root-cuttings are very like and probably identical with the variety called "Cardiff." Both type- and root-forms may have more colour than appears in the figures, especially in newly opened flowers, but the relative amounts of colour are correctly represented. In Mrs Gordon the guide-marks are only distinguishable as "ghosts."

Pearl is a white semi-double Regal (Pl. XIV, fig. 5) having small and evasive purple patches in the area of the guide-marks. Sir W. Lawrence kindly gave me a plant of Pearl having a large branch with flowers heavily marked with red (Pl. XIV, fig. 6) much as in the varieties known as Mme Thibaut and Emmanual Lias (? synonymous). Three root-cuttings raised from Pearl all have exclusively flowers of this coloration. Doubling in parent and the root form is similar in degree. Pearl itself has been grown here on a fairly large scale. At various times three flowers have been produced by it with a patch of red as shown in Pl. XIV, fig. 7. These patches must be regarded as indicating a break through of the underlying tissue, like the green patches so often seen on the leaves of some variegated chimæras composed of a white cortex overlying a green core.

The three examples mentioned are the only cases in fancy Pelargoniums of root-cuttings differing from parent plants up to the present. Numerous varieties have been tried, but at first we were not very successful in raising such plants. The technical difficulties have now been largely overcome, and we have a large series which will flower in due course. Plants identical with the parent have been raised from

Lady Doreen Long (1); Queen Alexandra (1); Kingston Beauty (several); and from Touchstone, a scented-leaved Pelargonium (12).

Pelargonium (Zonal).

Though no root-cutting has yet been raised from it the properties of a salmon, fringed zonal raised by Messrs Jarman and by them called "Golden Flame" (Pl. XV, fig. 1) should be considered here. The leaves of this variety are shiny, stiff and crumpled or buckled. Its flowers have laciniated petals and are devoid of functional female organs, the pistil being reduced and the ovary aborted. The anthers are normal, containing abundant and good pollen. The plant is therefore a male. Upon these plants not rarely a shoot arises which has leaves flat, with a dull matt surface like that of most leaves of zonals. On such shoots the flowers are normal hermaphrodites, and the petals are entire. Occasionally leaves otherwise of the characteristically crumpled kind have areas, small or large, of the sport variety.

Miss Cayley has supplied the following notes on the differences in structure between the two kinds of leaves:

Macroscopic Characteristics of Leaves

	Type (shiny)	Sport (dull)
1. Surface, upper	*Shiny*	*Dull*
Surface, lower	Dull	Dull
2. Size of leaf	Smaller	Larger
3. Shape	Somewhat ivy-leaved: crumpled	Typical zonal leaved: flat
4. Lobes of leaf	More acutely pointed	Rounded and more obtuse
5. Substance of leaf	Stiff	Soft
6. Hairs, upper surface	Numerous, but fewer than on the "sport"	More numerous than on the "type"
	Somewhat erect	Markedly bent towards the periphery of the leaf
	Thinner than the sport, but slightly longer	Somewhat coarser
7. Hairs, lower surface	Somewhat erect	Not so markedly bent, much the same as on the "type"
8. Petiole	Stiff	Less stiff
	Shiny	Dull
	Somewhat shorter	Longer
	Hairs less coarse but erect	Hairs coarser but erect

Microscopic Characteristics of Leaves

	Type	Sport
1. Cuticle	4–5μ thick	2–4μ thick
2. Surface of upper Epidermis	Flat. In section the outline is straight except at bases of hairs	Irregular: in section outline wavy

3. Surface of lower Epidermis	No clear difference: somewhat wavy in outline	
4. Epidermal cells: upper	Small: *with both upper and lower cell-walls thickened*	Larger: *no thickening of lower cell-walls*
5. Epidermal cells: lower	No clear difference	
6. Palisade cells	Elongated in vertical plane: compressed together, and regular in shape	Shorter, wider, less crowded and less compressed: more irregular in shape
7. Layers of palisade cells	Variable. 1–3 layers	Less variable: mostly one layer, occasionally more than one
8. Spongy parenchyma	No clear difference	
9. Bases of hairs	Raised	More raised than in type

When shiny and dull areas exist in the same leaf all stages of transition from the typical form to the other occur very irregularly. The change from thick cuticle to thin cuticle can be fairly abrupt, but the change in the shape of the palisade cells is more gradual and very irregular. A few "sport" palisade cells can occur in areas of "type" tissue and *vice versâ*, and the differences are not so clearly defined in the internal tissues as might be expected from the external appearance of the leaf. The fixation of the transitional parts is difficult, and no good microtome preparations have so far been obtained. The two types of tissues react differently with the same fixative; the "sport" tissue is penetrated more rapidly than the "type" tissue, and hence is fixed sooner than the "type."

The shiny appearance of the short leaf is possibly due to:

(1) Thickness of cuticle.

(2) Flat surface of the epidermis.

(3) Fewer hairs which are more erect and somewhat finer as compared with the bent hairs of the sport.

The darker green appearance of the same leaves is probably due to:

(1) Longer, more densely packed palisade cells.

(2) Extra layers of palisade which occur somewhat irregularly.

D. M. Cayley.

The inclusion of cells belonging to either form within the tissues of the other is especially remarkable.

Spiræa ulmaria.

A variegated form has stems, petioles, and central parts of the leaflets devoid of chlorophyll (Pl. XV, fig. 2), and of a whitish yellow colour. Ordinary green plants are perfectly fertile on both male and female sides, but this variegated plant is quite sterile, forming no

seeds or pollen. A few ill-formed carpels have been found on it, but the seeds they contained were aborted and did not germinate. The condition is closely reminiscent of the zonal Pelargonium, "Freak of Nature," mentioned in *Journ. Gen.* VIII, 1919, p. 97, *note*[1], which has green borders to leaves and stipules and is totally sterile on both sides. The extraordinary feature of that plant is that the green, white, and green-over-white shoots which Freak of Nature often produces are perfectly fertile. The variegated Spiræa has not hitherto produced any shoots other than those described. From its roots it readily gives rise to adventitious buds, and all leaves borne by them are albino, quite destitute of chlorophyll, like the stalks and petioles.

In my previous article on root-cuttings I spoke of the dissimilar forms which arise as being in all probability included as "cores" within a cortex of the ostensible type. The whole plant is thus regarded as a periclinal chimæra, one variety enclosing another, and this enclosed form may be expected to come out whenever the plant makes an adventitious bud by endogenous growth. Though this view is presumably correct in most cases the distribution seen in the variegated Spiræa and Freak of Nature shows that other possibilities must be remembered. For in these plants the white tissue is not covered in, but extends through the whole of the internodes, and doubtless the root also. The growing point alone carries up with it the power of making green tissue. In such plants as the *Bouvardia* or Pelargoniums which give dissimilar root-cuttings the two kinds of tissue are not recognisably distinct in the plant until they flower, and though perhaps unlikely, it is not impossible that the kind which arises by adventitious buds may really provide the *whole* of the root and perhaps the internodal regions. Many herbaceous variegated plants arranged periclinally are liable to give shoots composed entirely of either their external or their internal constituents. Such shoots with special frequency arise near the base of the plant, *i.e.* just above the level at which the stem was divided in propagation. Though their mode of origin is not always easy to decide, it must be supposed that they are generally produced by adventitious buds. These evidently are not always endogenous but may be originated by a periclinal division in the cortical layer.

In such an example as the crumpled zonal here described, or indeed in any periclinal chimæra with patches of its core coming out on the surface of leaves, the process by which this change is brought about

[1] [This volume, p. 286.]

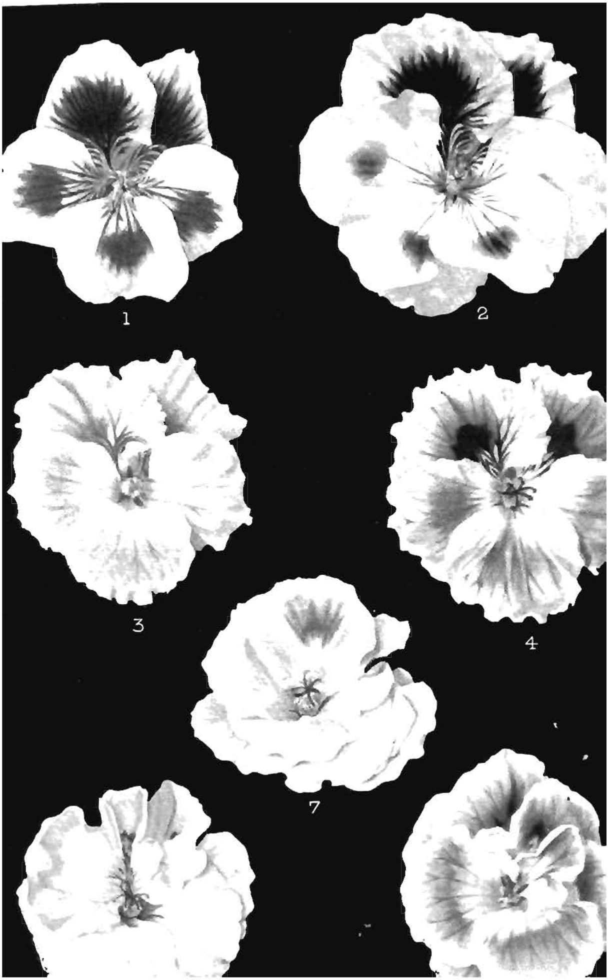
1
2
3
4
7

Fig. 1.

is very difficult to imagine and I do not know how it may be represented. The growing point must contain both elements, but the emergence of that which is normally enclosed seems at present to be purely fortuitous.

As regards *reversals* of the layers, such as I described in *Journ. Gen.* VIII, 1919, p. 94[1], it is worth observing that though we have now fairly numerous cases of white-over-green turning to green-over-white, a change which in some plants happens frequently, we have not hitherto seen a single instance of the contrary. Of *Euonymus*, some zonals, an ivy-leaved Pelargonium, and *Arabis* we have several large and well-grown plants of the green-over-white kinds, but though occasionally the white has come to the surface in a small area, no reversal has been found on such plants. Possibly we may regard white-over-green as an arrangement mechanically less stable than green-over-white.

Several attempts have been made to breed the root-cuttings with their parent plants, an experiment offering attractive possibilities, but we have hitherto been unsuccessful.

EXPLANATION OF PLATES

PLATE XIV

Fig. 1. Pelargonium Escot.
Fig. 2. Root-cutting of Escot.
Fig. 3. Pelargonium Mrs Gordon.
Fig. 4. Root-cutting of Mrs Gordon.
Fig. 5. Pelargonium Pearl.
Fig. 6. Root-cutting of Pearl.
Fig. 7. Flower with red blotch, a form occasionally seen on Pearl.

This plate is from drawings by Mr C. H. Osterstock. In the photograph the colours of Escot and the two forms of Mrs Gordon are approximately correct. In Escot's root-cutting the red should be distinctly brighter, without any bluish tinge, and the same applies to the red colour in Figs. 5 and 7.

PLATE XV

Fig. 1. Zonal Pelargonium Golden Flame. On the right is seen the foliage of the type, which is buckled and shiny. On the left the sport, with leaves flat and dull. The two right-hand inflorescences are laciniated. The two left-hand inflorescences bear mixed flowers, some entire, some laciniated. The fruits formed in two entire flowers are visible. These mixed inflorescences belonged to the area of transition.
Fig. 2. *Spiræa ulmaria*: leaf of variegated form.
Fig. 3. *Spiræa ulmaria*: leaf of normal green form.

[1] [This volume, p. 283.]

MALE-STERILITY IN FLAX, SUBJECT TO TWO TYPES OF SEGREGATION

(With Plate XVI)

[*Journal of Genetics*, XI, 1921]

In 1912 a single plant was noticed in a patch of *Linum grandiflorum* sown in our border of annuals. It was remarkable as having a blue flower and procumbent habit, whereas *L. grandiflorum* is deep crimson and erect. In its low stature the new plant somewhat resembles the various kinds of flax cultivated for oil in many countries. Several of these oil-flaxes have in subsequent years been grown here, but we had none in 1912, which was indeed the first year in which any form of *L. usitatissimum* was sown in this garden. All the flaxes cultivated, whether for fibre or oil, are included under that specific name. The new plant, which we shall here call the "procumbent," is also evidently a true *usitatissimum*, though in being procumbent it differs from any variety which we have seen. Obviously it has no connection with *grandiflorum*, which is a very distinct species. We have no surmise as to what its origin may have been, but somehow a stray seed from which it arose must have got mixed with the *grandiflorum*.

Since in 1912 experiments on flax were begun with various objects the appearance of the procumbent was a matter of interest, and its seeds were collected. Whether the flowers had been covered is not recorded. Probably they were, but the point is of little importance, for only a small percentage of crossing occurs in *usitatissimum*. The procumbent bred true from the first and has continued true in each year since, except that a naturally cross-bred plant appeared once in a row raised from unprotected seed, as may happen with any flax.

The new form differs from any other flaxes that we know in the following respects:

1. It is procumbent during growth, branching much from the base, and the stems reach about 2 feet in length, *lying at first flat on the ground*, turning upward as flowering begins, and finally standing more or less erect.

2. The style is *very pale* in colour, and when the petals of an opening flower are pulled off it projects well above the sepals, which are perhaps slightly shorter than those of ordinary flaxes. But like other

forms of *usitatissimum* the variety is definitely homostyled, the tops of the anthers just reaching beyond that of the stigma.

3. It is *very late in flowering*, about 10 days later than any other variety that we have.

In other respects there is nothing special to note. The capsule and seeds are of the ordinary size, not large as those of our oil-flaxes are.

The first crosses were made in 1916 by Miss M. Michell of Cape Town, who fertilised the procumbent with pollen from a tall white-flowered fibre-flax. The object of this cross was to study the genetics of height. Though from the extraordinary uniformity in height characteristic of *pure lines* of flaxes these plants seem well adapted for such work, the distribution of height in F_2 is complicated, all intergrades occurring, with indications of segregation so imperfect that useful results could only be obtained by measurements on a very large scale continued through several generations. Much work of this kind has been carried out on which we may publish a report later, but at present it must suffice to say that though segregation in respect of height occurs, and though the parental types, both procumbent and tall, reappear in F_2, they are rare, and the height-curves of these families show no obvious dimorphism.

The purpose of the present paper is to give the facts respecting the behaviour of a *male-sterile* form which appeared in F_2 in 1918. F_1 is erect and intermediate in height, and in colour also (as T. Tammes found[1] in crosses between blue and white flaxes, and as we have also often seen in other cases). In F_2 Miss H. Garlick, who was then in charge of these experiments, observed certain plants, both blue, white and intermediate in colour, which had flowers with reduced petals, as a rule scarcely opening at all. In these flowers the anthers are more or less completely aborted. A row of such plants growing beside a row of normally flowered flaxes is shown on Pl. XVI, together with photographs of drawings of the normal and of the abnormal flowers in various stages.

Varieties with aborted anthers are familiar in a great number of plants. Some, as for example that of the Sweet Pea, are quite sharply defined, others, as for instance that studied by Miss Pellew in *Campanula carpatica*, may exist in many intergrading forms. As in the Caryophyllaceæ and Labiatæ, such flowers may coexist in various grades on the same plant, and may even be associated with normal hermaphrodite flowers. In these and other Natural Orders flowers

[1] Tammes, T., *Rec. Trav. bot. Néerl.* VIII, 1911, pp. 264–5.

with aborted anthers are both by systematists and writers on genetics often referred to as females, and the species possessing them are called gyno-monœcious or gyno-diœcious as the case may be. It is not easy to apply any definition which will distinguish flowers or plants with aborted anthers from the normal female flowers of some diœcious species (*e.g. Lychnis*), but to avoid raising this theoretical question we propose to follow the usage of some American authors and call them male-steriles. In these flaxes the sterility of the anthers is nearly but not quite complete. No grades of plants were recognised beyond the ordinary hermaphrodites and the male-steriles, but anthers of the steriles occasionally reach a degree of development sufficiently complete to produce a little good pollen. Flowers with this low degree of male-fertility may be found sporadically, as it seems, on any male-sterile plant. From their pollen a few seeds have been obtained in self-fertilisation which gave rise again to male-steriles only. No degree of male-sterility was ever observed in the flowers of ordinary flaxes. In the breeding work it was not thought necessary to emasculate the male-sterile flowers, and in only one mating (Expt. 5) is there reason to suppose that disturbance was caused by their pollen.

In previous experiments on the genetics of male-sterility the male-steriles were introduced as an already recognised type. In our work they arose in F_2 from a cross between two fully hermaphrodite types. Subsequent experience proved that the new form was brought in by the pollen of the common flax, and that the procumbent is genetically hermaphrodite on both male and female sides. Twenty-four fibre-flax plants of various kinds (Expts. 6–10) tested by using their pollen on male-steriles, gave in all 640 plants, all male-steriles. To these 24 which gave a uniform result may be added the white plant, from the male side of which the original F_2 family containing male-steriles was derived, and a tall blue plant on similar grounds (Expts. 1 and 2).

One tall plant (Expt. 11) used as male on a male-sterile gave a hermaphrodite. If authentic, this constitutes a single exception to the rule that the pollen of normal flaxes carries the male-sterile only. Whether it should be discarded as an error or not we cannot yet say. It came in a family containing only two plants, the other being a male-sterile.

From the evidence of these 26 plants we must conclude that the *fibre-flaxes in general, perhaps always, are heterozygous in respect* of the male-sterile allelomorph, and that in segregation this allelomorph is relegated to the male side.

As regards oil-flaxes we have only preliminary indications and can make no statement as yet.

The procumbent itself is clearly hermaphrodite in genetical composition on both male and female sides. The male side was tested as follows. Tall × procumbent (Expt. 3) gave from 3 F_1 plants 559 all ☿ in F_2; white × procumbent similarly gave 157 ☿ in F_2 (Expt. 4); also male-steriles fertilised by procumbents (3) gave 101 ☿, and also 2 male-steriles (Expt. 5) which may safely be assumed to have arisen by self-fertilisation, the mother-plant not having been emasculated.

But when the procumbent is used as mother and fertilised with pollen from a fibre-flax, F_1 is a normal hermaphrodite, and in F_2 the *male-steriles appear as 1 in 4. It is proved therefore that the female side of the procumbent must in some way be different in constitution* from the female side of the ordinary flaxes. In heterozygosis with the female of the procumbent the dominant factor for anther-development passes with its negative allelomorph to both male and female organs of the offspring, thus producing an ordinary Mendelian result, but when the same negative is in heterozygosis with the female side of the common flax, it passes wholly to the pollen, evidently segregating not later than the constitution of the sexual organs. The ordinary flax, though heterozygous, is thus able to breed true just as *Begonia Davisii* does for singleness (though heterozygous for doubleness) and as the various Œnotheras investigated by Renner may do, though heterozygous for several complexes.

In connection with this example the somewhat cognate evidence discovered by Miss Pellew in *Campanula carpatica* should be recalled. There also very similar plants were shown to possess distinct types of segregation in respect of the same negative allelomorph. The case of the flaxes differs from that of the *Campanula*, for in that example the plants in which both allelomorphs went to both sexual sides showed an irregular distribution, whereas here they follow a normal Mendelian system. It will be interesting to see whether a cytological basis for these phenomena can be detected.

Attempts to use the male-steriles *as males* in crossing have hitherto failed, the pollen produced by them being very small in amount.

Much interest would attach to the genetics of plants made in such a way that the male-sterility was brought from the *maternal* side into combination with one or other of the hermaphrodite factors introduced from the paternal side. Various possibilities are thus opened up. On these questions we have as yet no sufficient evidence, Expt. 19

being the only one bearing on the point. There the hermaphrodite element was that of the female side of procumbent, and it was brought in from the male side of a plant homozygous in F_3 or a homozygous F_2. Tried on a male-sterile it gave 6 male-steriles and 1 ☿. That it should have given the ☿ is worth noting, but work on a large scale is required to explore the many alternative distributions which will possibly be encountered. Material for these investigations is being prepared.

Plants in which the distribution of factors differs on the two sexual sides of the same plant now form such a prominent subject of genetical consideration that some simple terms are required to facilitate discussion. We suggest that in the ordinary Mendelian distribution the segregation might be called *ambilateral*, effected on both sexual sides of the plant, as distinguished from the *unilateral* segregation which carries the allelomorph wholly to one sexual side[1].

In other examples, e.g. the double-throwing single in *Matthiola*, we might speak of the segregation as partially unilateral. The exception mentioned above (Expt. 11) may indicate that here also the unilaterality may on occasion be partial, but unless the phenomenon recurs its significance is doubtful.

Details of Experiments

P = Procumbent. *MS* = Male-sterile.

The "tall" strain is that first raised here by selection[2]; "Dark blue" is another raised since; "Dark blue tall" is another, now pure, raised by combination of the above.

Expt.	☿	*MS*
1. From P × white, 3 F_1 plants gave in F_2	53	9
2. From P × tall, 4 F_1 plants gave in F_2	308	100
Totals	*361*	*109*
3. From tall × P 3 F_1 plants gave in F_2	559	—
4. From white × P 3 F_1 plants gave in F_2	157	—
Total	716	—
5. *MS* × *P*		
5 mothers × 3 fathers gave	101	2
The 2 *MS* resulting were doubtless due to self-fertilisation		

[1] *Proc. Roy. Soc.* 1920. [2] *Journ. Gen.* v, 1916, p. 199. [This vol., p. 261.]

MS × various fibre flaxes.

Expt.		Parents used ♀	Parents used ♂	Offspring ☿	Offspring *MS*
6.	*MS* × tall	15	16	—	402
7.	*MS* × dark blue tall	2	1	—	57
8.	*MS* × dark blue	5	3	—	72
9.	*MS* × white	5	3	—	77
10.	*MS* × Canadian fibre	1	1	—	32
	Totals	28	24	—	640

11. In addition to these was the exceptional case in which *MS* × a tall gave 1 ☿ and 1 *MS*.

F_2 plants from Expt. 2 were tested as follows:

Expt.		☿	*MS*
12.	Two ☿s selfed gave F_3	98	30
13.	Two *MS* × two sister ☿s (1 used in Expt. 12) gave proving that these ☿s were heterozygous	14	12
14.	One *MS* × sister ☿ gave proving that this ☿ was homozygous	41	—
15.	5 ☿s from Expt. 13 selfed gave	378	140
16.	4 ☿s from Expt. 5 selfed gave	298	87
17.	4 *MS* × sister ☿s gave	58	58
18.	2 ☿s of complex origin (derived from *P* ♀) gave	43	25

Adding families derived from *P* ♀, which are expected on selfing to give 3 : 1, there are

Expt.	☿	*MS*
1.	53	9
2.	308	100
12.	98	30
15.	378	140
16.	298	87
18.	43	25
Totals	1178	391

Adding those expected to give 1 : 1

Expt.	☿	*MS*
13.	14	12
17.	58	58
Totals	72	70

Expt.

19. Case mentioned, p. 331.

	☿	*MS*
MS × ☿ from Expt. 14 (viz. a plant which had received *MS* from maternal side and hermaphrodite factor from the paternal side) gave	1	6

EXPLANATION OF PLATE XVI

Fig. 1. A row of male-sterile plants (left) growing beside a row of normal plants (right).

Figs. 2–8. Drawings of flowers with petals and sepals removed; Figs. 2–4 and 6 from blue-flowered plants; Figs. 5, 7 and 8 from whites.

Fig. 2. Normal just before opening.

Fig. 3. Same later, anthers dropped.

Fig. 4. Male-sterile, unopened flower, the usual condition.

Fig. 5. Rarer condition of male-sterile, unopened flower. Stamens more developed, occasionally bearing some pollen.

Figs. 6–8. Later stages of male-steriles. Anthers shrivelled but persisting.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

GENETICS OF *PRIMULA SINENSIS*

(With Plates XVII–XXIV)

[*Journal of Genetics*, XIII, 1923]

At the time of his death in 1918 R. P. Gregory was continuing the experiments on *Primula sinensis* which had occupied him since 1903. He published a paper in 1911 giving several results already arrived at, and subsequently notes dealing with special points. These publications however represent only a small part of the ground covered by his work, which in 1918 had already extended over many features not previously reported on at all. During his lifetime the plants were grown partly at the Cambridge Botanic Garden and partly at the John Innes Horticultural Institution. Those at Cambridge were, during the war, mainly in the care of Miss Killby, who carried out the manipulations. At Merton the work was undertaken by various members of the staff, especially Mr Backhouse, the late Mr E. J. Allard, Miss I. Sutton, Miss Thornton, also by Miss A. Sverdrup, and several other volunteers; but for some part of each year Gregory attended and recorded the results himself. After his death the Cambridge experiments were wound up, and the Merton section was somewhat extended. So much of the work we have now to describe owed its inception to Gregory, or has grown out of material with which he dealt, that his name most properly stands at the head of the present publication.

Some 18 pairs of characters have been investigated more or less fully. They relate to the forms of the leaf; the forms of the corolla; the anthocyanin colours and their distribution in vegetative structures, petals, and the gynœcium, especially the stigma; the extent of the yellow pigment surrounding the "eye" of the flower; the heterostyle condition; single and double flowers.

Interactions have been observed between factors affecting primarily the leaf-shapes, and those producing distinctions in the corolla-shape. Crimping of the leaf, for instance, is associated with fringing of the petals, the tongue-shaped leaf with an elongation and narrowing of the petals[1], etc. These are associations which might be expected, but the intensification of the crimping which results when the *sinensis*

[1] The "oak" leaf causes a frequent deformation of *sinensis* flowers if single, but this effect is not noticeable in doubles or in the *stellata* forms (see Figs. 33 and 34).

flower is transferred to the crimped leaf is curious. The most remarkable of these interactions is that between the factors governing the extent of the yellow eye and those affecting the margin of the leaf. This mass of interactions, involving three distinct sets of characters (petal shape, eye, leaf margin), has not yet been completely analysed. An outline of the facts is included in this paper. The essential points are:

(1) The normal eye is not compatible with the crimped leaf which entails some extension of the eye.

(2) The most extended eye (that called "Primrose Queen") is compatible with a perfectly flat leaf; but when this eye is combined with a slightly crimped leaf, the crimping is intensified.

A good deal of information has been acquired as to the giant varieties, some of which are tetraploid, and as to defect of chlorophyll in the leaves, etc., but these two subjects are not treated of in the following paper.

Material

The bulk of the plants were derived in part from those which had been experimentally bred in Cambridge since 1903, and in part from Messrs Sutton's collection. We acknowledge gratefully the constant assistance we have had from Messrs Sutton, who have put their experience unreservedly at our disposal. We have also to thank Messrs Carter for a set of their double-flowered oak-leaf variety which was brought into the work in 1916.

Besides these forms which are more or less familiar greenhouse objects, we received in 1913 a plant hereafter spoken of as "Lee's" which is new. Mr E. Lee, then of the Botanical Staff at the Birkbeck College, since killed in the war, called in 1913, bringing a plant with some novel characteristics. He said that this form had appeared spontaneously in the vinery of a private garden at Egham, and had since bred true. The edges of the palmatifid leaves were much *crimped* (details below). In correspondence with this peculiarity the petals were minutely crenelated. These crenelations were like those in the ordinary *sinensis* flower, but more numerous and more regular, giving the corolla a fringed appearance. The flowers were *double*, this doubling being of the peculiar kind called by Gregory (1911, p. 90) "ordinary" (*i.e.* for modern strains), in which each petal bears an extra limb arising at the mouth of the tube, standing in the reversed attitude characteristic of this type of doubling. The yellow eye was

large, but in double flowers the exact nature of the eye is often ambiguous. The colour was pale *mauve*. The fringe made the flowers look like *sinensis* in shape[1], and the colour was taken to be of the magenta class. Subsequent breeding showed that the shape was *stellata*, and that the colour was genetically red: for crossed with red *stellata* single, F_1 was red *stellata* single, and all the later history was consistent with this determination. The eye proved to be altogether peculiar. When combined genetically with singleness (Fig. 35, *D*) it was found to be a broad yellow eye, slightly less extensive than that of Primrose Queen (P.Q.), but the greatest extension is not central (as in P.Q.) but lateral, so that the yellow patch is in each petal bilobed. Moreover, whereas in P.Q. the style does not, in long-styled plants, rise above the anther-ring, the style of Lee's comes to the top of the tube as usual.

Both in crimping, colour, shape of flower, and eye-structure, Lee's is distinct from any variety hitherto known, and its spontaneous occurrence constitutes a mystery. Crimping in a slight degree occurs in two other varieties whose peculiarities will subsequently come up for consideration.

It seems at first that whatever variety may have been the immediate parent of the Lee's type, several factors must have been lost in its origin. This however is not a true inference. The crimp of the leaf and the fringing of the petals have, as might be expected, proved to be genetically inseparable, and are due to the loss of one factor. Also all attempts to combine the ordinary small "eye" with the crimped leaf have failed, though either form of large eye, whether the Lee's or the P.Q. sort, is compatible with it. Lastly the light pink of the corolla always has a mauve tinge when the leaves are crimped, so much so that accurate sorting of reds from magentas is almost impossible in a crimped class which contains both. Hence the distinctive features of Lee's may reasonably be attributed to the loss of a single factor only.

Forms of the Leaf

In referring to these we use the terms *palm*, *oak*, *fern*, and *crimped*. They are controlled by three allelomorphic pairs, of which none are linked to each other. All the combinations have been now made except one which is doubtless equally possible (fern, crimped).

[1] On crimped leaves we find that *sinensis* can always be distinguished from *stellata* by the possession of the much inflated calyx with ten or more teeth, not five as in *stellata*.

Palm is the normal palmatifid shape.

Fern (*Fig. 21*) *is a familiar recessive to it* (Gregory, 1911, Pl. XXX, fig. 7). Factorially these are represented as *P* and *p*. To determine precisely the powers of *P* is not quite easy. In its absence the width of the leaf is much reduced and the shape becomes pinnatifid. The whole number of chief divisions of which the leaf consists is somewhat increased. Apart from minor serrations, the apical lobe is trifid in each. This in the palm is succeeded on each side by two lobes each nearly as large as the apical, posterior to which is a large lobe almost always recognisably divided into four subordinate parts, the posterior edge being free from the petiole and forming a flounce at the base of the leaf. In the fern the apical lobe is succeeded on each side by *three lobes about as large as the apical, behind which is a series of some* five or more lobes decreasing successively in size, arranged as a set of decurrent pinnæ arising directly from the petiole. The whole number of lateral lobes is thus larger in the fern, being about eight on each side, as against six in the palm, counting the four subordinate divisions of the large posterior lobe separately. Of course, as in all similar examples, these numbers may differ in different plants and in the leaves of different ordinal positions, but the numerical distinction is clear in any pair of well-grown leaves occupying comparable positions. The minor serrations are also distinctly more numerous in the fern leaf. The palm and fern leaves may perhaps be *said to differ somewhat as the 5-rayed limb of the mammal differs* from the many-rayed fin of the fish.

Oak is a form known in horticulture under that name (Figs. 22 and 25). It also is a simple recessive to palm. The number of lobes is smaller than in palm. Posterior to the anterior portion, which might be taken to represent the trifid apex of the normal, there is a deep sinus which comes in nearly to the midrib. Next follows on each side a large serrated and partially bifid lobe, separated posteriorly by a still deeper sinus from a similar large and bifid lobe. This posterior lobe is always so completely separated from the rest of the leaf as to constitute an independent leaflet. The serrations are much fewer than those of the normal palm.

At the apex of each serration is a hydathode, or water-pore, which is figured in Jost's *Plant Physiology*, trans. by Gibson, Oxford, 1907, p. 57. The number of serrations is therefore that of the hydathodes. In view of what follows, information as to the exact mode of origin of these structures is desirable.

A comparison between the lobing and the serrations in palm, fern, and oak (all *flat* leaves, not crimped) is given in the following tabulation. The numbers are those of the serrations counted in a well-formed and characteristic leaf. Each lobe is given separately (cf. Figs. 24 and 25) and the brackets indicate the grouping of the subordinate lobes into the larger ones.

Normal Palm (*e.g.* "*Etna*")

Group	Left	Apical	Right	Group
		15		
	13	—	12	
	17	—	14	
14 {	9	—	9	} 26
	6	—	6	
	4	—	5	
	5	—	6	
	54	15	52	

Total 121

Fern

Left	Apical	Right
	13	
9	—	10
12	—	10
13	—	13
17	—	13
12	—	13
9	—	14
7	—	7
4	—	8
83	13	88

Total 184

Oak

Group	Left	Apical	Right	Group
		9		
13 {	9	—	10	} 15
	4	—	5	
17 {	11	—	8	} 14
	6	—	6	
	30	9	29	

Total 68

Fern and oak are simple recessives to palm. Fern × oak gives F_1 palm, and in F_2 the combination fern-oak appears. Homozygous palm has not yet been raised from this cross, though presumably this could be done. *Fern-oak*, in addition to the apical lobe, has on each side *about four large lobes and two small ones at the base. Serrations* in it have been observed as follows:

Left	Apical	Right	
	6		
6	—	7	
8	—	8	
9	—	9	
9	—	6	
2	—	3	
1	—	2	
35	6	35	Total 76

Between each lobe there is a deep sinus, as in the palm-oak.

The details given by no means completely represent the leaf-shapes even of flat forms. For instance one of the palm-leaved varieties, "Czar" (blue, with coloured gynœcium), may have as many as 165 points, but the width of the leaf in this variety is considerably greater than that of the normal and the margin lies flat. By small distinctions between the leaves, an accustomed eye could probably recognise most

of the pure-breeding strains. Such details we have not attempted to analyse.

Crimped forms. In Lee's, which was our original crimped, the edges of the (palm) leaves bear a great number of points each with a hydathode, which commonly, if not perhaps always, is connected with a vessel. Each of these has evidently the power of independent growth uncoordinated with that of the limb of the leaf as a whole. The margin is thus enormously increased and crimping results. These little lobes have varied shapes (Figs. 26 and 27), most often forming lancet-like processes with parallel edges, but often also widening out at the sides so that the hydathode stands as the cusp of a widely curving bracket. The processes overlap each other irregularly and the consequent crumpling of the edges of the leaf turns them downwards in greater or less degree. The normal division of the main lobes is preserved, and these are as usual one apical, and on each side two more, with a broad more or less quadripartite lobe posterior to them.

This crimping is quite distinct from that of such plants as parsley, curly kale or some forms of *Scolopendrium.* In them, owing to the multiplication of points, the edge of the leaf is much extended with consequent crumpling, but there is no development of small, minor lobes or processes as in these Primulas. Analogous developments may however be seen in *Begonia manicata*, var. *crispata. Teucrium Scorodonia* has also a somewhat similar variety, which was the subject of a paper by M. C. Rayner[1].

In the original Lee's, a *stellata*, the number of points is about 630, that of a normal flat palm being about 120–130; but when the *sinensis* flower is combined with the crimped leaf the number is enormously increased. The points are then difficult to count accurately. We have counted at least 1440 in a leaf of this kind.

The combination of crimped leaves with *sinensis* flowers involves another peculiarity. When such plants are about a year old some at least of their leaves become excessively crimped, the edge of the leaf being prodigiously elongated, so that it is greatly contorted. Their leaves become so much folded as to hang almost like balls from their petioles (Fig. 36). From the fact that the points cannot be counted on the same leaf both when young and again when old, the question is difficult to decide quite positively, but we have little doubt that leaves of this combination have the power of developing new points as they grow older. On such a leaf (Fig. 19) at about 18 months old,

[1] *Journ. Gen.* VII, Pl. X.

in which the development was by no means extreme, 7000 points were counted, and doubtless much higher numbers occur. A bit of the edge of this leaf is shown in Fig. 27 magnified. The hydathodes which, when they develop, constitute the "points" are visible in such leaves at all stages of development, from slight bulges in the outline to finger-like elongations. They are *not* present in the sinuses between the chief points. Such developments have, we suppose, been studied by botanists, but we know no literature bearing on the subject.

Whether all the leaves on these plants are capable of increase in the number of hydathodes we cannot say. The change is much more striking in some than in others. The appearance might perhaps be due to the development and increase in size of points already predetermined as rudimentary hydathodes, but from the presence of many still rudimentary in these old leaves, we incline to believe that an increase in number actually occurs. Nothing suggestive of this phenomenon has been seen in the leaves of any other combination.

Crimping combined with *oak* shape also increases the number of points, but in much less degree. Crimped-oak (*sinensis*) has about 96–100, instead of the 70 of flat-oak.

Besides the much crimped Lee's variety we have lately begun to work with a strain grown by Messrs Sutton which exhibits crimping in so low a degree as at first sight to be scarcely comparable. This (Fig. 30), which we call *Sutton's crimp*, has about 235 points to the leaf with distinctly noticeable marginal imbrication. From the fact that this form has the same influence on the eye (though in a lower degree) as Lee's has, there is no doubt that it is essentially similar.

Under the name "Moss-curled" Messrs Sutton cultivate still a third type, with leaves crimped slightly, but in a definite and peculiar way. From various indications we infer that this variety is cytologically distinct, having an excess of chromosomes. In crosses with the normal, signs of genetical incompatibility appear. As to its factorial composition no statement can yet be made.

Though the *sinensis* flower makes an enormous difference when transferred to the Lee's crimped, giving it about 1440 instead of the 630 characteristic of the corresponding *stellata*, there is no corresponding distinction between the flat leaves when combined with either of the two flower-shapes, *sinensis* and *stellata*.

Apart from the novel phenomena of interaction to which allusion has been made, the genetical interrelationships of the leaf-shapes are not altogether what might be expected. The small number of lobes

and points in palm dominates over the larger number in fern, whereas *the still smaller number of divisions of both kinds in the oak is re*cessive to the larger number in palm. Possibly the critical distinction in the oak is really the formation of the deep sinuses, with a decrease in number of divisions consequent upon it. The curious form described by Gregory (1911, p. 87) as "ivy," which has long ago been lost, though possessing the usual number of major lobes had a smooth, undivided edge. It also was a recessive to palmate. That there should be simple dominance in all these cases is in itself remarkable. Commonly in other plants the heterozygote between a less cut type and a much cut variety is intermediate. (Shull's *Capsella*; *Hibiscus* bred here, etc.) Evidently the interrelations of the *Primula* leaf-shapes are of a different nature, and the subject might repay investigation in greater detail[1].

The Eye of the Flower and its relation to Crimping of the Leaves

Gregory showed that the normal small yellow eye is dominant to the large eye of Primrose Queen (P.Q.). This peculiar form in which the yellow extends up over about a third of the limb of the petal was figured by him in Pl. XXX, fig. 12 (see also our Fig. 35, *C*). The white eye of "Queen Alexandra" (*ibid.* Pl. XXX, fig. 11, etc.), in which the yellow colour is almost totally suppressed, proved to be in varying degrees a dominant over both the other two types. Heterozygotes in this case are sometimes easily recognised as such, but by no means always. The character is interesting as the only one, besides the dominant white, which we must regard as an addition to the make-up of the species since it arrived in Europe.

The Lee's variety introduced a new type of eye, in which the yellow is only a little less extensive than in Primrose Queen, though the two can be immediately distinguished by the position of the stigma, which is normal in Lee's but below the anthers in P.Q. Lee's eye is recessive to the white eye, but is dominant over the P.Q. eye.

[1] Another form of the leaf exists in one of Messrs Sutton's strains of the "Duchess" colour to which they now give the name "ivy." As it is quite distinct from the old "ivy" with which Gregory worked we prefer to call it "tongue," a name which fairly well describes the shape of its elongated little-cut leaves. Petals on tongue-leaved plants are never normal, being elongated, and narrowing towards the periphery, somewhat as the leaves do. A similar alteration in the petal-shape in connection with the leaf-shape is mentioned above as seen in the crimped forms. We have not yet worked with the tongue strain.

The white eye, the normal, and the P.Q. eye form a series of multiple allelomorphs, in this descending order (Fig. 35). They are three quantitative stages in the amount of yellow. The third term never appears in the descent from crosses of the other two, if pure. Complication is introduced by the special relations in which these forms of eye stand in regard to the crimping of the leaves. The limiting and obvious facts are:

1. The normal eye is never combined with the fully crimped leaf.

2. The P.Q. eye is compatible with the flat leaf, but the Lee's eye is not. Since the P.Q. eye has a greater extension than the Lee's this is unexpected.

3. P.Q. flat × Lee's crimped gives F_1 normal eye, flat leaf.

F_2 consists (7 families) of *flat* leaves, with eyes normal *or* P.Q.; and *crimped* leaves, with eyes Lee's *or* P.Q.

The cross of Lee's crimped by P.Q. flat has given F_2 families as follows:

Reference number	Flat		Crimped	
	Normal eye	P.Q. eye	Lee's eye	P.Q. eye
156/20	96	35	9	5
99/20	8	2	1	—
104/20	30	8	7	4
110/20	27	15	3	3
83/22	19	11	15	3
84/22	42	13	10	6
87/22	106	38	32	12
Totals	328	122	77	33

These numbers are very irregular, though suggesting the ratio 9 : 3 : 3 : 1, which gives the expectation *315 : 105 : 105 : 35.* The subsequent history is consistent *qualitatively* with this representation inasmuch as

(1) Lee's crimped (het. in P.Q.) × P.Q. crimped gave 74 Lee's, 54 P.Q., all crimped.

(2) F_1 flat normal (from Lee's crimped × P.Q. flat) × Lee's crimped gave 345 flat, normal eye, 215 crimped, Lee's eye.

(3) F_2 flat, normal eye (het. in P.Q.) × flat P.Q. gave 260 normal eye, 250 P.Q. eye, all flat.

(4) Lee's eye, crimped (het. in P.Q.) × flat P.Q. gave 62 normal eye, 72 P.Q. eye, all flat.

In each case equality of numbers is expected, from which several

results depart widely. Such numerical irregularities are frequent throughout this work (see the section on this subject) but the classes produced are those we expect. In addition to those given, we have the results from various derivatives selfed, which are all confirmatory. Homozygous *flat* leaves with normal eyes have not yet been bred as derivatives from these matings, but presumably that could be done without difficulty.

From these facts we conclude that the Lee's eye is genetically identical with the normal eye, but that it is modified and extended when in combination with the crimped leaf. If this were all we might say simply that the effect of the crimped leaf is to extend the eye. Therefore we should anticipate that the P.Q. eye also, when on the crimped leaf, would be even further extended. P.Q. flowers in this combination however *are always somewhat deformed* (Figs. 11, 31, 35, *E*), having the edges of the petals more or less rolled inwards, with a very narrow free limb. The appearance suggests that the eye is enlarged, but in such flowers no very strict standard of comparison can be applied.

We now meet a further complication. Since the P.Q. eye produces no noticeable effect on the normal flat leaf it was with surprise that we found that in F_2 from Sutton's crimped × P.Q. flat, those plants which combined the P.Q. eye with the crimped leaf were so much crimped as to be indistinguishable from the Lee's crimped type itself (see Figs. 31 and 28). Were it not that their eye was P.Q. and not Lee's, we might have imagined that Lee's was again newly arisen in this recombination. It should he observed that the P.Q. eye has no noticeable effect on the crimping of Lee's, but only on that of the less crimped type. At present we know no parallel to this mutual influence of two such dissimilar features upon each other.

The "Old Double" Type

The late Mr E. J. Allard devoted great labour to obtaining a cross with this type. The petals are indefinite in number, succeeding each other in imbricate fashion and entirely replacing the stamens of which no trace remains. Almost always the stigma, if present, is split open, the ovules in the gynœcium being exposed. Such flowers of course produce no seed. By repeated fertilisation with singles two seeds were successfully produced on a flower in which the deformity was presumably not so extensive, and subsequently a third from a distinct cross. According to the record the male parent in the first

case was a short-styled *tetraploid*[1], the second having been an ordinary diploid. There is no reason to doubt the record, but if authentic it is the solitary instance of a successful cross between diploid and tetraploid plants. The strain derived from the cross was lost long since and no further evidence about the cytology exists.

This imbricate type of doubling behaved as a recessive, recurring in somewhat irregular proportions.

The original F_2 consisted of 26 singles, no doubles. The absence of doubles is consistent with the belief that the male (single) was tetraploid, for only one double in 16 would be expected. But the F_2 from the cross with the single, which was certainly diploid, gave 33 singles, 2 doubles, again a notable shortage. The subsequent families in each set showed no special departure from a 3 : 1 expectation.

The imbricate double is *possibly* linked with the style-form, whether long or short. In these double flowers, which have no anthers, the condition of the style cannot be readily told by direct observation; but since the first cross was made with a short-styled father, and longs reappeared, the double must have been genetically long-styled.

The Harlequin Type

In F_2 from the cross imbricate double × diploid single a very peculiar new type appeared which we call *Harlequin*. In it, one, two, or rarely three of the petals are fully or almost fully coloured (whether red, magenta, or otherwise), the other petals being white or whitish. The coloured petals are of the full size, whereas the pale petals are smaller in various degrees, being sometimes much reduced in size. This type has occurred in both the *stellata* shape (Fig. 15) and also in the *sinensis* shape (Fig. 14). The deeply coloured petals, in the folding of the flower-bud, are internal. This fact suggested that possibly the pale colour of the outer petals was due to some special sensitiveness to the action of light, but flower-buds covered with black paper at an early stage showed no diminution of the "Harlequin" effect. Harlequins always breed true in their peculiarity which behaves as a simple recessive.

Blue Flowers

The genetical relations of blue flowers to the rest have hitherto been obscure. From the fact that plants, ostensibly blue, had been

[1] Namely, a Giant. At that date no cytology had been attempted, but the strain to which this plant belonged has since been proved to be tetraploid.

bred both from magentas and from reds, blue was regarded as recessive to those colours. It has now been established that of the flowers which we have accepted as blue, some, to which in future we shall restrict the term blue, possess a positive factor, *B*, which is absent from the others. These last we shall call *slaty*. Their colour, at least when in combination with the ordinary, light reddish stem, is recognisably distinct from that of the real blues, though on casual inspection the two may easily be confused. Microscopically examined they are seen to be perfectly distinct. In the blues the anthocyanin of the epidermis of the petals is in solution (Fig. 3), whereas most of the cells of the epidermis of slaty flowers *contain anthocyanin in a solid form*[1] (Fig. 4). Occasionally the appearance of these anthocyanin bodies suggests a crystalline structure, but more often they are amorphous. Not rarely two or more may occur together in the same cell. Sometimes dissolved anthocyanin is associated with the solid bodies, but many cells in which they are present seem to be otherwise colourless.

It is the slaty plants which are recessive to both magenta and to red. Real blues cannot be bred from reds. Factorially the relations of the colours may be represented thus:

Magenta *BR*.
Red *bR*.
Blue *Br*.
Slaty *br*.

All the available genetical evidence is consistent with this account. The interrelations of these colours to the *coral* ("Orange King" of Gregory's paper, Pl. XXX, fig. 8) have not been completely determined, but a form nearly resembling coral exists which is recessive to slaty.

In association with the dark red stem, both the blue and the slaty are modified and assume a very peculiar appearance. This is represented in Figs. 7 and 8. No uniform blue or slaty has been seen on the dark stem, and such flowers are presumably an impossibility in that combination. The petals of such plants, both blue and slaty, apart from a uniform zone round the eye, are mottled, and the general tint is distinctly redder than that of the corresponding flowers on the light stems.

We have now to regard the factors *B* and *R* as both possessing the property of keeping the anthocyanin in solution and making its

[1] In the vegetative parts of these plants no solid anthocyanin has been met with.

colour *blue* or *red* respectively. It should be mentioned that on fading, certain red flowers (*e.g.* that shown in Fig. 13) produce solid *blue* anthocyanin in the dying cells[1]. A peculiar type in which the petals are irrorated and mottled with red has occasionally appeared as a rare derivative from certain crosses. The general colour of these is that called strawberry (Gregory, Pl. XXXI, fig. 49 and p. 113). In one such plant which remained in the collection when these examinations were made, solid *red* anthocyanin, in part crystalline, was seen.

As a corollary to what has now been ascertained, it follows that, when *magenta* has been spoken of as linked with other allelomorphs, it is really the factor B which should be so represented.

Linkage Groups

Two linkage groups have heen identified. The first was recognised about 1907 as a special association of *magenta* flowers with the *green* stigma. As now explained the factor which actually takes part in this linkage is B, blue. Subsequently it was found that short style, S, is included in the same linkage. To these was afterwards added L, the factor for the light reddish stem and leaf-backs, as opposed to its absence, l. Plants without L have these parts a deep, claret-red (see Figs. 1 and 2). Leaves of such plants, even seen from above, are intensely dark.

The four factors involved in this linkage are:

S, short style as opposed to s, long style.

B, blue as opposed to b, no blue.

(The factor R, causing red flowers, is probably not included in this linkage group.)

G, green as opposed to red stigma.

L, light reddish as opposed to deep red stems.

At the time of Gregory's publication coupling and repulsion had been observed as affecting this group of factors and it has since been established that they are interrelated as an ordinary linkage group. The system however exhibits one remarkable peculiarity, the first

[1] Whether all have this property is not certain.

We have looked for solid anthocyanin in "blue" primroses of various tints, but found none. Mr R. J. Chittenden however called our attention to abundance of solid anthocyanin in the living epidermis of petals in a dark brown Polyanthus.

Gertz, quoted by Wheldale, *Anthocyanin Pigments of Plants*, 1916, p. 33, has seen solid anthocyanin in stems of *Primula sinensis*. Studier öfver Anthocyan, *Akad. Afhandling*, Lund, 1906, p. xlii.

indication of which was detected by Gregory (1911, p. 128). As we now know, in two of the linkages involved, ***the closeness of linkage differs greatly in the male and female sides of the same plants.*** This was suspected from the F_2 numbers, and has been proved by extensive back-crossing. The linkages are as follows. The values, whether as coupling or as repulsion, are the same.

	Observed linkage		Percentage of cross-overs	
	Female	Male	Female	Male
SB	12·2 : 1	7 : 1	7·5	12·5
SG	2 : 1	1·5 : 1	33·3	40
SL	1·7 : 1	1·47 : 1	37	40·7
BG	2·2 : 1	1·9 : 1	31·25	34·5
BL	1·8 : 1	1·7 : 1	35·6	37
GL	29·6 : 1	52·4 : 1	3·2	1·8

It will be noticed that the linkage of *S* with *B* is closer on the *female* side, whereas that between *G* and *L* is closer on the *male* side. We are not aware that similar sexual distinctions have been met with elsewhere. In animals the evidence is that crossing-over does not occur at all in the heterogametic sex, so no comparison can be instituted. In plants we are now familiar with wide differences between the genetic composition of the gametes on the two sides of heterozygous plants, but a sexual difference in closeness of linkage has not, so far as we know, been observed.

Bridges (*Amer. Nat.* 1914, XLVIII, p. 532), taking Gregory's numbers for the linkages between the three factors here called *S*, *B*, *G*, tabulated them according to the chromosome theory. At that date reciprocal back-crosses had scarcely been undertaken and the problem to which they introduce us was not then apparent.

On the theory that crossing-over takes place during a side-to-side conjugation between the parental chromosomes this new fact presents a grave difficulty, since the loci at which the same factor must, on the theory, be supposed to stand, will be different in the male and female chromosomes. These loci will therefore not be at the same levels in the conjugating chromosomes. The hypothesis might perhaps be amended by the introduction of some conception of orderly looping in synapsis, but this supposition would be difficult to verify and recourse to it would throw a considerable strain on the theory.

Judged from their microscopical appearance, the pollen grains of these Primulas are normal, and defective grains are as exceptional as in any pure species.

SECOND LINKAGE GROUP

Linkage has also been found between the following two pairs of factors, which are not linked to any of the first group:

F, flat leaf as opposed to *f*, crimped leaf.

Ch, *sinensis* flower as opposed to *ch*, *stellata* flower.

The value of this second linkage is 8·6 : 1, or 10·4 per cent. of cross-overs. This value is the same on both the male and female sides. The numbers from self-fertilisation, though showing irregularities, are not inconsistent with this estimation, though a shortage of crimped plants is sometimes conspicuous.

As regards the lower degrees of crimping, the evidence shows that "Sutton's crimped" is subject to the same linkage as the more fully crimped Lee's form.

The observed numbers, upon which these statements as to the linkages are based, will be found tabulated at the end of this paper.

NEW COMBINATIONS

In the absence of the factor *G*, the gynœcium, and especially the stigmatic surface, is coloured, being usually red, and several flower colours only reach their full development in plants which are without *G*. No fully red petals (Fig. 12) for example, and no dark blue ones (Fig. 5) are ever formed on plants which possess *G*. The combination of these fully coloured flowers with the deep claret-coloured leaves, which are formed in the absence of *L*, had not previous to these experiments ever existed. From the horticultural point of view that combination offered great possibilities. To obtain it was one of the objects Gregory had in view, and from the theory of linkage it could readily be inferred on inspection of the F_2 from $Gl \times gL$ that the combination could be made. As the linkage is high, about 30 : 1 on the female side and about 50 : 1 on the male side, the required plant could only occur about once in 6500 F_2 plants. For some years no progress was made, but in 1915 a plant was noticed which had red stigmas combined with leaves somewhat redder than the ordinary "reddish" form. This was suspected of being heterozygous in *L*, and on selfing it produced the plants required. Usually the heterozygotes cannot be distinguished. Plants of the new combination were handed over to Messrs Sutton, and after some purification in other respects, were exhibited by them at the Royal Horticultural Society's Shows in 1921, and listed under the name "Etna." The new combination

makes various others now attainable. Since this is perhaps the first practical result which has accrued from an application of the theory of linkage, the occurrence seems to be worth recording.

Unfortunately the combination of fully blue flowers with Etna foliage appears to be a physiological impossibility. Such flowers, with coloured stigmas, are characteristic of the well-known variety Czar, which of course, containing L, has leaves of the lighter colour. $\left.\begin{matrix}\text{Czar} \times \text{Etna} \\ Bg\,Lr \quad bg\,lR\end{matrix}\right\}$ gives F_1 Magenta, with light foliage. F_2 from this has given us the expected series Magenta, Red, Blue and Slaty on each of the two types of foliage, but as explained in the section on blue flowers, the genetically blue-flowered plants with Etna foliage have the blue colour much mottled and are scarcely recognisable as blues. The factor B in this series showed the same linkage with L as in other experiments, but having been obtained after the section on linkage was prepared these families have not been brought to account.

A Peculiar Mosaic

Colour-mosaic flowers occur sparingly. Amongst others we have for example seen magenta flowers with a radial stripe of red, or of blue, and pale magenta with a stripe of deep magenta. Each of these shows loss of a factor in the area affected, respectively B, R, or the element for lighter colour. Special importance attaches to a plant in two flowers of which a stripe has appeared showing the loss of *two* factors. The plant was magenta, green stigma, P.Q. eye, and the stripe in each case was the type due to the absence of B and G, being deep red of the kind seen only in combination with red stigma (see Figs. 16, 17, and 18). No flake of colour was visible in the stigma, but the gynœcium was not examined since it was hoped to raise seed from the flower.

As B and G are linked, it is of interest to observe that in this remarkable mosaic these two factors have fallen out together. The plant may be and probably is heterozygous in these two respects.

Numerical Ratios

Departures from numerical expectation are common in many sections of this work. They were noticed long ago among families raised by self-fertilisation, but since, by the work of a staff, back-crossing has been rendered feasible on a considerable scale, the results

so attained have emphasised the impression previously formed. Adequate treatment of this subject is beyond the scope of this paper. It would involve much tabular printing and the application of statistical methods with which we are unfamiliar.

A few specimens of the numbers we have met with are included, with a report on them most kindly supplied by Dr G. Udny Yule, F.R.S.

To have much value such an investigation should deal collectively with the numbers recorded for divers characteristics in a great variety of organisms. Experience of such numbers suggests that, apart from numerical aberrations due to differential mortality and comparable interferences, there are significant distinctions between various organisms in this respect, some following closely, others departing more often from the numerical equality which may be regarded as the normal consequence of simple Mendelian segregation. We are disposed to attribute some at least of these departures to definite sporadic events whereby, of the two kinds of gametes with contrary powers, one has become more numerous than the other. It can happen but rarely in practice that more than one breeding test can be applied to the same aberrant plant. We have only one instance which supplies such evidence. Three families were raised by self-fertilisation from apparently similar plants, heterozygous in stigma colour as follows:

1922	Green stigma	Red stigma
Number 39 gave	109	33
Number 42 gave	125	45
Number 44 gave	100	8

39 and 42 may each be taken as obviously 3 : 1, but 44 gave about 12 : 1. It happens that the parents which produced these offspring by self-fertilisation were also back-crossed with the recessive, giving the following results:

	Green stigma	Red stigma
39^3/21 parent of 39/22 as ♀	27	29
39^3/21 parent of 39/22 as ♂	29	29
39^4/21 parent of 42/22 as ♂ (not tried as ♀)	9	14
40^1/21 parent of 44/22 as ♀	62	22
40^1/21 parent of 44/22 as ♂	39	15

These figures prove that the parent of 39/22 was normal on both sides in the equality of gametes bearing the two allelomorphs, that

the parent of 42/22 may have been similarly normal, but tbat the parent plant from which 44/22 was derived was almost certainly abnormal on both sides.

Taking 62 : 22 as probably indicating 3 : 1 on the ♀ side and 39 : 15 as suggesting 2 : 1 on the ♂ side, we should expect a ratio of 11 : 1 on self-fertilisation, which is approximately the ratio produced (*99 : 9* where 100 : 8 was observed).

Usually such aberrations are noticed too late for any check to be applied. In cases of abnormal ratios we have often tested the resulting plants, but have found no recurrence of the aberrant numbers. Gregory (1911, pp. 84–5) records however an instance of this kind where the short-style gametes were greatly in excess throughout a related group of plants[1].

As specimens of the general run of the numbers we give three examples. Dr Udny Yule has examined these series and prepared a report on each which we are permitted to incorporate. The first relates to plants heterozygous in three pairs of factors, *sinensis*—*stellata*; green stigma—red stigma; white ("Alexandra") eye—ordinary yellow eye. All were back-crossed with triple recessives. In 16 families the heterozygote was the mother, in 6 the fatber.

The results are given in tabular form. Simple expectation of course is that the eight numbers in each column should be equal. The families 110 and 131 are especially abnormal. Gregory devoted much study to such examples. In his opinion they strongly suggested that whether by successive segregation followed by proliferation in special groups of segregates, or by some other process, significant inequalities in the resulting numbers were produced not uncommonly. Whatever the source of the inequalities, we are disposed to regard them as representing a definite physiological phenomenon. In 110 for example the *sinensis* group (56) is more than double the *stellata* group (22), and we think it likely that either proliferation has occurred in the one or an inhibition of division in the other, such that the ovary was probably in a state analogous to that of a mosaic plant or branch.

Nevertheless we see no indication of regularity among these aberrant numbers. Sometimes one group, sometimes another is in excess; nor, on the analogy of mosaicism, would regularity be expected. Dr Yule reports as follows:

[1] On p. 125, *ibid.* we find there was an error in copying from the record. In the last line the figure "17" should have been "10," which weakens the argument advanced in the text.

Triple heterozygote ♀ × triple recessive ♂

		Reference number	54	55	58	59	107	110	119	121	122	127	129	131	132	133	135	178	Totals
Sin.	gr. stig.	wh. eye	5	18	17	2	12	17	9	10	24	9	3	16	20	9	11	10	192
		yell. eye	10	13	11	12	20	16	10	7	23	3	6	24	18	2	13	12	200
	red stig.	wh. eye	4	10	17	3	14	10	6	8	19	5	5	23	18	10	7	12	171
		yell. eye	9	17	11	11	13	13	9	8	9	6	3	12	18	1	9	12	161
Stell.	gr. stig.	wh. eye	13	22	20	10	5	5	16	2	30	3	8	21	19	4	9	12	199
		yell. eye	14	16	18	9	12	6	14	3	16	5	7	13	14	4	13	10	174
	red stig.	wh. eye	10	11	12	6	7	3	18	2	11	5	4	14	23	4	6	13	149
		yell. eye	7	12	16	6	10	8	10	4	23	5	4	22	23	7	8	16	181
		Totals	72	119	122	59	93	78	92	44	155	41	40	145	153	41	76	97	1427
		Value of P	0·20	0·35	0·60	0·072	0·085	0·0076	0·18	0·090	0·012	0·68	0·68	0·24	0·87	0·048	0·65	0·96	

Triple heterozygote as ♂ crossed with triple recessive ♀

		Reference number	60	63	64	94	95	97	Totals
Sin.	gr. stig.	wh. eye	11	11	10	28	7	7	74
		yell. eye	10	8	6	28	4	7	63
	red stig.	wh. eye	16	4	5	24	2	10	61
		yell. eye	9	7	11	26	5	7	65
Stell.	gr. stig.	wh. eye	18	13	15	19	6	14	85
		yell. eye	10	12	12	29	10	12	85
	red stig.	wh. eye	8	12	11	26	4	11	72
		yell. eye	13	14	14	24	7	7	79
		Totals	95	81	84	204	45	75	584
		Value of P	0·398	0·317	0·317	0·898	0·387	0·570	0·695

"The chances for the several families of getting a series of deviations from expectation (uniformity) as bad as or worse than those observed (obtained by the χ^2 method) are as follows:

Female heterozygote		Male heterozygote	
54	0·20	60	0·40
55	0·35	63	0·32
58	0·60	64	0·32
59	0·072	94	0·90
107	0·085	95	0·39
110	0·0076	97	0·57
119	0·18		
121	0·090		
122	0·012		
127	0·68		
129	0·68		
131	0·24		
132	0·87		
133	0·048		
135	0·65		
178	0·96		

The first series of families, in which the female was the heterozygote, is clearly significantly divergent from expectation. A family as badly divergent as 110 would only be expected on random sampling once in some 1300 trials. If sampling were random the values of the above chance, usually denoted by P, should be uniformly distributed over the range 0 to 1. They are not at all uniformly distributed and 6 of the values are less than 0·1, whereas only 1 or 2 (one-tenth of 16 or 1·6) should be less than 0·1. The average value of P for this series is only 0·358 instead of 0·5.

The second series, in which the male was heterozygous, shows no evidence of anything abnormal: no value of P is very low, and the average is 0·48, or very near the theoretical 0·5.

For the totals of the first group of families P is 0·17, for the totals of the second group 0·69. This is confirmatory of the conclusion as to the greater abnormality of the first group. It looks as if the abnormalities were in the ovules rather than the pollen.

Reverting to the first series of families, it will be seen that while family 131 catches the eye owing to the regular distribution of its divergences, the value of P is not very low (0·24). But if the distribution of the characters for each pair (A, sin.: B, stigma: C, eye) are taken out, these distributions, and the ratios for the single characters,

are all very near the expected equality. The oddity only comes out when the three characters are taken together.

When family 110 is taken in the same way it will be seen that the ratio of $A : a$ is altogether abnormal (56 : 22); you would not expect such a divergence on random sampling more often than once in some 8000 trials or so, but the ratios for B and C are much nearer normality. Correspondingly, for the three pairs of characters in this family the values of P are

AB	0·00061
AC	0·0012
BC	0·60

A (the sin.: stell. pair) is apparently the source of abnormality.

Similar investigation of family 122 suggests that B (stigma) is the source of abnormality. The ratio $B : b$ is 93 : 62 and the values of P are low for the pairs AB and BC (0·085 and 0·028) but quite high for AC (0·63).

Family 133 is small and one would hardly expect to get anything very clear out of it, but C (eye) looks like the source of trouble. The ratio $C : c$ is 27 : 14 and the pairs AC, BC give the lowest values of P, the pair AB being quite a good fit. It is a curious accident that, taking these three abnormal families, each suggests an abnormality arising from one of the three characters only, and a different character in each case. There are probably not more than 4 or 5 abnormal families out of the 16 altogether, judging from the run of the P's—assuming of course that the families can be definitely sundered into normal and abnormal."

We also submitted to Dr Yule the records (too extensive for publication here) of 211 families in which plants heterozygous for short-style (thrum)—long-style (pin) had been back-crossed with recessives, and of 331 families similarly tested for magenta—red. Many of the heterozygous parents are common to both series, and they represent tests of both ovules and pollen indiscriminately. He has furnished the following report:

"The *totals* cannot be regarded as diverging significantly from equality though the divergences are a little uncomfortably large: the number of thrums differs from expectation (4090) by 1·79 times the standard error and the number of magentas differs from expectation (6739·5) by 1·65 times the standard error. But in view of the fact, which comes out very clearly on examining the figures for correspond-

ing families in the two records, that S and B are highly linked if the one character shows a rather large divergence from expectation the other is almost bound to: the results are not independent.

I have examined the data as regards the fluctuation of the proportion of dominants amongst the families. I sorted out the families with 50 plants or more [52 for thrum—pin; 99 for magenta—red], listed them separately, worked out the percentage of dominants in each, and booked up the frequency distributions, which are given in

Percentage	Number of families showing said percentage of *S*	Number of families showing said percentage of *B*	Percentage	Number of families showing said percentage of *S*	Number of families showing said percentage of *B*
37	1	—	55	3	1
38	—	1	56	6	4
39	1	—	57	—	6
40	—	2	58	—	3
41	1	5	59	1	5
42	1	2	60	1	2
43	1	4	61	—	2
44	4	6	62	—	1
45	—	1	63	—	1
46	1	3	64	—	—
47	6	9	65	—	1
48	1	4	66	1	—
49	2	5	67	—	—
50	7	6	68	—	1
51	4	7	69	1	—
52	3	10	70	—	—
53	4	4	71	—	1
54	2	2			
			Totals	52	99

the table above. The standard deviations of these distributions compare as follows with the standard deviations of sampling:

	Observed S.D.	S.D. of sampling
Thrum	5·97	5·76
Magenta	6·59	5·79

In both distributions the observed standard deviation is greater than the S.D. of simple sampling, the excess being the more marked for the 'Magenta' series, *i.e.* the fluctuation is rather greater than is theoretically expected.

As regards the form of the frequency distributions, the only thing to be noted is that they are exceedingly irregular, as will be seen from the table. The *similarity* of the peaks in the two distributions suggested some significance, but this is probably only due to the linkage and th

fact that the 'Magenta' distribution contains the majority of the families in the 'Thrum' record. There is an odd symmetry about the peaks however. If the distribution is doubled over round 50 per cent. so as to add the frequencies for 51 and 49 per cent., 52 and 48 per cent. and so on, the peaks stand out even more clearly than before.

As regards specially exceptional families, I have not made a detailed examination, but 106/12 [64*B*, 30*b*] and 103/12 [76*B*, 114*b*] in the 'Magenta' series caught my eye. The chance of such a divergence from equality occurring is about 0·0005 for the first and 0·006 for the second. The small family 38/12, with 15*B* and 2*b* only, is also very divergent—the chance of such a divergence occurring on random sampling being only about 0·0023.

There is nothing, unfortunately, clear-cut and definite—but, wider fluctuation than there ought to be, distributions irregular, and irregularities slightly suggestive of something definite, and some markedly exceptional families, and that seems about all one can say."

Pending a comprehensive examination of such numbers collected from various sources it is, as we have said, not possible to assert positively to what degree those that we have given are unusual, but we are inclined to think that the amplitude of divergence from normality differs considerably in the various subjects studied and perhaps also in regard to special factors. As the comparison with mosaics may naturally be made, it should be added that mosaics in the somatic tissues are by no means common in *P. sinensis*. An occasional flake of a recessive colour in the flower is not very uncommon and sometimes *stellata* petals may appear on plants heterozygous for *sin.—stell.*, but even these mosaics in general are rare. *A flower mosaic in colour is figured (Fig. 16) and discussed on p. 350.*

The History of *Primula sinensis*

In view of the genetical interest of the species an accurate account of its origin is greatly to be desired. Unfortunately little is positively known as to the circumstances in which it was first seen in China, and we have no acceptable surmise as to its wild progenitor or progenitors. The first evidence of the existence of such a plant reached Europe in the form of a drawing received from China by the Royal Horticultural Society in 1819. At their request seeds and a plant were dispatched by Mr [John] Reeves who procured them in Canton, but the plant died and the seeds failed to germinate. Shortly after, a

plant was brought over successfully by Capt. Richard Rawes "from gardens" at Canton.

In 1821 two coloured plates were published by Ker-Gawler (*Bot. Reg.* Pl. 539) and by Lindley (*Collectanea Botanica*). Whether both represent the original plant is not clear. More probably they were made from its immediate offspring. Both show the flowers as magenta of the shade associated with a green stigma, and both in flower-shape approach *sinensis*, though to an observer accustomed to these plants, they are almost certainly of the type called by Messrs Sutton "*pyramidalis*," viz. heterozygous in respect of the *stellata* shape. Being *sinensis*, they have ten calyx-teeth, and Lindley had some doubt whether, in view of this peculiarity, the plant was rightly referred to the genus *Primula*. In accordance with the ideas of the period the suggestion was made in *Bot. Reg.* that this might be the effect of "luxuriance"!

W. J. Hooker (*Exotic Flora*, II, 1825, Pl. 105) gives a very good coloured figure, this time of the *stellata* type with five calyx-teeth, and a less satisfactory drawing of a similar plant was published in *Bot. Mag.* 1824, tab. 2564. Mention is made of the *sinensis* type with ten calyx-teeth as coexisting with the *stellata* form. Of the plants figured in these plates four were certainly and all may have been short-styled. In all the leaves are palm[1].

Another early reference is made by Lindley (*Trans. Hort. Soc.* VI, 1826, p. 80) who, after speaking of Rawes's first importation, states that plants raised from seeds afterwards brought from China by Mr Potts, one of their collectors[2], were distributed by the Society.

This second importation is not usually quoted in histories of the plant. Since, however, Lindley in 1826 explicitly states that the plant was known to him in two varieties [*sinensis* and *stellata*] we may be fairly sure that nothing ostensibly fresh was raised directly from Mr Potts's seeds.

The original plant therefore had nearly all the dominant factors yet identified. Two only have been gained since: the dominant white which inhibits the formation of anthocyanin in the petals, and the white or "Alexandra" eye which inhibits the yellow of the normal

[1] The leaves in Lindley's plate, said to have been drawn by W. J. Hooker, are curiously different from any we know. Probably this is due to imperfect drawing.

[2] The Librarian of the Roy. Hort. Soc. kindly showed us a MS. diary of Mr Potts's Chinese experiences, but we found in it no mention of *Primula*.

eye. The white eye was introduced by MM. Vilmorin about 1902, but no details are known as to the origin of either of these two dominants.

As regards variation by loss, it is clear that the *stellata* form appeared at once, the original being heterozygous for it. The same is probably true of the long-style. Good notes of the cultural history are given by A. W. Sutton[1] with dates at which novelties were noticed or developed. Many were the result of deliberate cross-breeding, especially those brought out by Messrs Sutton, one being especially noteworthy—the "Duchess" type—as evidently due to a breaking up of the dominant white. It has petals white peripherally with a red band round the eye. This is figured by Gregory (1911, Pl. XXXI, figs. 27–8). As he stated, the periphery of the corolla alone is white, the complementary part of the dominant-white complex which controls the gynœcium and the centres of the petals being absent. "Duchess" cannot therefore exist with a green stigma, for that would enable the white to invade the centre of the flower.

Usually little can be established as to the variations by which the original factorial composition has been changed. The fern-leaf appeared early in the cultivated history, and the crimped or crispated leaf several times. Perhaps the clearest evidence relates to the colour known as "orange" or "coral," which is known to have come by loss of a single factor, without crossing, from the crimson called "Crimson King," a type which had been bred, on a very large scale, true for many years. Blues, derived from magenta by loss of the factor R, and the large "Primrose Queen" eye, are among the latest recessives to appear.

The question arises, what were the plants first seen by Mr Reeves in China, and whence did they come? The statement made in *Bot. Reg.* is that Capt. Rawes brought the plant "from gardens at Canton, where it probably found its way from some far more northern quarter of the country." This implies that *P. sinensis* was then already in cultivation by the Chinese, but repeated inquiries from competent botanists acquainted with China have failed to elicit anything as to such plants being at present in cultivation there. Mr W. Tutcher of the Botanical and Forestry Dept., Hong Kong, kindly wrote (1910) that old gardeners there remembered growing it thirty years before, but can add nothing more. We have also letters, which Dr A. Henry and Mr George Forrest were good enough

[1] *Journ. Roy. Hort. Soc.* XIII, 1891, p. 99.

to send us, containing negative information[1]. Dr Henry directed us to a figure in a modern Chinese Botany, *Chih Wu Ming*, XXIX, p. 18, which might possibly represent the *stellata* form. We are obliged to Mr Waley and Mr Giles of the British Museum for a translation of the text, which is unfortunately inconclusive. The plant in question was from Yunnan. Its leaves and bracts are described in terms suggestive of *sinensis* rather than of any other species that we know, but till some collector finds this plant, its nature must remain ambiguous.

As the originals were in "gardens" they *may* have had a history of hybridisation behind them. The production of such a series of novelties coming into existence within so few generations is scarcely to be paralleled by any pure-bred species of plant. On the other hand there is no indication of infertility at any time (except in connection with tetraploidy), and though varieties came, they seem to have appeared sporadically over a period of years. Disintegration consequent on hybridisation is a very different process.

The nearest parallel is perhaps to be seen in the Sweet Pea (*Lathyrus odoratus*), though in it the structural variation has been very much less. *Primula obconica*[2] also has given rise to several types differing chiefly in colour and size, but nothing approaching the multitude of forms known in *P. sinensis* has appeared, and *P. malacoides*[2], though it also has produced varieties, is by comparison a fixed species.

The history of the three species of Primula agrees moreover in the fact that though many crosses have been tried with all of them not one is known to have been successful. The various records of alleged positive results are almost certainly erroneous, and there is scarcely a doubt that these plants are all genuine examples of spontaneous variation, almost always by loss of factors, occurring without crossing, under domestication. To those familiar with modern genetics it is scarcely necessary to point out that spontaneous variation is not the common occurrence we formerly thought it to be, and in the history of cultivated plants the Sweet Pea and *P. sinensis* stand out as probably the two best authenticated examples of this phenomenon manifested on a large scale.

We used to regard the Sweet Pea as a plant above suspicion of

[1] A letter to the same effect has lately been received from Mr F. Kingdon Ward, well known for his collections of Chinese plants.

[2] Evidence collected by A. W. Hill, as to *P. obconica*, *Journ. Gen.* II, 1913, p. 1, 2 Plates; and as to *P. malacoides*, *ibid.* VII, 1918, p. 193, 2 Plates.

having undergone crossing. Trials with numerous species of *Lathyrus* are known to have resulted in failure. Successes have been reported from time to time but the accounts have been insufficient, and in view of the species used[1], and the ease with which errors may occur, unconvincing. In 1916, however, Barker[2] gave a full account of a cross between Sweet Pea Kitty Clive fertilised by *L. hirsutus*, which produced fertile F_1 plants, giving segregation at least in colour and size in F_2. Any chance that the Sweet Pea could have been crossed during its early history with *hirsutus* or any other species is however so remote that we need scarcely hesitate to accept its variations as the spontaneous developments of a pure species.

As regards the Sweet Pea, *P. obconica* and *P. malacoides*, there is no difficulty in tracing them to the single wild original species. Till some wild species is found from which *P. sinensis* can have been derived, we cannot be perfectly certain that no crossing has occurred, but the presumption is against that supposition.

Of the vast number of wild species which have been brought from China none really resembles *sinensis* to the eye of any one intimate with that plant. Mention must be made of a curious mistake which was made in this respect. A species was found by Mr Walters and later by Dr Henry and the Abbé Delavay at Ichang on the Yang-tze river, which was taken first by Dr Masters and afterwards by other distinguished botanists for the original *P. sinensis*. Under that name it was figured in *Bot. Mag.* (1897, tab. 7559) where many particulars are given. No one seems to have doubted about it. There are nevertheless definite differences. The shape of the leaf is quite distinct from all the leaf-shapes known in *sinensis* both in lobing and the crenelations of the margin. The leaves are hard to the touch. Their surface has a fine very short and even pubescence, not the pilose ciliation of *sinensis*. The bracts and calyx are also different, and the scent of the foliage is quite distinct[3]. Besides these features which

[1] For example, a cross with *L. pratensis*, *Gard. Chron.* I, 1913, p. 173; with "*L. luteus aureus*," *ibid.* p. 85.

[2] *Gard. Chron.* 1916, p. 156. Mr S. C. Harland recently informed us that he has independently made this cross and has F_2 seeds.

[3] The *Bot. Mag.* plate shows the petals covered with hairs. These however are not present in the plant. They appear, though less conspicuously, in the original drawing which Mr A. W. Hill has shown us and must have been put in by mistake. In the plant (as in *sinensis*) there are glandular hairs on and close to the yellow eye, but the limb of the petals is glabrous.

Since this was written the name *Primula calciphila* has been proposed for the species in question (see *Gard. Chron.* 1923, p. 101, Fig. 49).

can be expressed in words, there is a difference in substance and general appearance which to those accustomed to handle *sinensis* is very clear, and though *à priori* no one could deny that the Yang-tze species might conceivably have been one of the parents of *sinensis*, there is no question of identity. It is not even surprising to us that all attempts to cross that species with *sinensis* have failed. The capsules swell but no seed is formed. With its own pollen it has so far bred true to type. Cytological examination has not yet been made.

Subsequently a species was collected by Farrer[1] which has a somewhat closer resemblance, such indeed that we anticipated that crosses with it might succeed. We have not had this plant, but crosses tried at Kew have failed.

Finally we must recognise the problem created by the *ten*-toothed calyx associated with the *sinensis* shape of the flower as originally introduced. Ker-Gawler compared the flower to that of *P. cortusoides*, but it seems that no wild species is yet known to have the ten calyx teeth. This depends on the presence of a definite dominant factor. The heterozygote, though often recognisable as such, is so like pure *sinensis* that batches of the pure and heterozygous forms cannot be sorted with confidence. The *stellata* by contrast is—when combined with a flat leaf—clearly distinguishable. We must therefore admit the likelihood that this dominant *sinensis* factor has been added since domestication though before the plant left China.

NUMBERS OBSERVED IN THE LINKAGE SERIES

First Linkage Group

Factors involved:

S, short-style in the absence of which the style is long (*s*).

B, blue flowers in the absence of which the flower is slaty (*b*) [unless *R* the factor for red is present].

G, green stigma and gynœcium in the absence of which these parts have anthocyanin (*g*).

L, stems and leaf-backs light red in the absence of which these parts are deep red (*l*).

On the chromosome theory the "order of the genes" would be as above, *S, B, G, L*.

[1] It has received the name *P. rupestris*, Balf. f. et Farrer. I. Bayley Balfour, *Trans. Bot. Soc. Edin.* xxvii, 1918, p. 240.

Data for linkage SB[1]

♀ $\frac{SB}{sb} \times sb$

	SB	*Sb*	*sB*	*sb*	
	120	17	10	109	
	1250	102	82	1287	from matings involving also *G*
	152	16	24	159	,, ,, *L*
	146	13	12	148	,, ,, *G* and *L*
Totals	1668	148	128	1703	

Linkage on female side 12·2 : 1, *or* 7·5 % *of cross-overs*

[1] The data include those previously published by Gregory. It should be understood that numbers taken from matings involving factors other than those dealt with in any particular group reappear also in the groups relating to those other factors.

Further data on the linkages between *S*, *B* and *G* were obtained by Altenburg (*Gen.* I, p. 354 and *Amer. Nat.* LV, 1921, p. 78) on material supplied by Gregory. These figures are not here included.

♀ $sb \times \frac{SB}{sb}$

	SB	*Sb*	*sB*	*sb*	
	147	20	20	157	
	770	102	106	643	from matings involving also *G*
	586	72	83	580	,, ,, *G* and *L*
Totals	1503	194	209	1380	

Linkage on male side 7 : 1, *or* 12·5 % *of cross-overs*

$\frac{SB}{sb}$ selfed

	SB	*Sb*	*sB*	*sb*	
	156	18	11	57	
	72	2	4	15	also involving *G*
	198	12	8	61	,, *L*
	1897	91	122	620	,, *G* and *L*
Totals	2323	123	145	753	
Expectation	*2346*	*159·7*	*159·7*	*675·5*	

Calculated on {♀ *linkage* 12·2 : 1. ♂ ,, 7 : 1.

Data for linkage SG

♀ $\frac{SG}{sg} \times sg$

	SG	*Sg*	*sG*	*sg*	
	70	35	45	56	
	896	430	440	914	also involving *B*
	99	60	66	98	,, *B* and *L*
Totals	1065	525	551	1068	

Linkage on female side 2 : 1, *or* 33·3 % *of cross-overs*

♀ $sg \times \frac{SG}{sg}$

	SG	*Sg*	*sG*	*sg*	
	31	28	21	33	
	535	331	315	428	also involving *B*
	391	267	266	397	„ *B* and *L*
Totals	957	626	602	858	

Linkage on male side 1·5 : 1, *or* 40 % *of cross-overs*

$\frac{SG}{sg}$ selfed

	SG	*Sg*	*sG*	*sg*	
	49	15	10	7	
	60	14	11	8	also involving *B*
	287	70	83	55	„ *B* and *L*
Totals	396	99	104	70	
Expectation	*401·4*	*100·3*	*100·3*	*66·9*	

Calculated on {♀ *linkage* 2 : 1, ♂ „ 1·5 : 1.

$\frac{Sg}{sG}$ selfed

	SG	*Sg*	*sG*	*sg*	
	1367	*537*	*532*	*114*	*also involving B and L*
Expectation	*1360*	*552·5*	*552·5*	*85*	

Repulsion calculated as above

Data for linkage SL

♀ $\frac{SL}{sl} \times sl$

	SL	*Sl*	*sL*	*sl*	
	212	*125*	*130*	*234*	
	90	58	54	88	also involving *B* and *G*
Totals	302	183	184	322	

Linkage on female side 1·7 : 1, *or* 37 % *of cross-overs*

♀ $sl \times \frac{SL}{sl}$

	SL	*Sl*	*sL*	*sl*	
	72	56	57	102	
	387	265	273	387	also involving *B* and *G*
Totals	459	321	330	489	

Linkage on male side 1·47 : 1, *or* 40·7 % *of cross-overs*

$\frac{SL}{sl}$ selfed

	SL	*Sl*	*sL*	*sl*	
	99	35	32	12	also involving *B*
	1578	375	549	230	„ *B* and *G*
Totals	1677	410	581	242	
Expectation[1]	*1727·7*	*454·8*	*454·8*	*272·7*	

Calculated on {♀ *linkage* 1·7 : 1. / ♂ „ 1·47 : 1.}

$\frac{Sl}{sL}$ selfed

	SL	*Sl*	*sL*	*sl*	
	273	84	126	12	also involving *B* and *G*
Expectation[1]	*266*	*105·2*	*105·2*	*18·6*	

Repulsion calculated as above

[1] The departures from expectation on selfing are here and elsewhere perhaps noteworthy in view of the comparative regularity of the results of back-crossing.

Data for linkage BG

♀ $\frac{BG}{bg}$ × *bg*

	BG	*Bg*	*bG*	*bg*	
	1186	509	511	1051	
	926	381	410	963	involving also *S*
	202	93	112	176	„ *L*
	140	69	66	142	„ *S* and *L*
Totals	2454	1052	1099	2332	

Linkage on female side 2·2 : 1, *or* 31·25 % *of cross-overs*

♀ *bg* × $\frac{BG}{bg}$

	BG	*Bg*	*bG*	*bg*	
	247	120	141	250	
	584	267	284	474	involving also *S*
	96	50	59	90	„ *L*
	423	241	231	417	„ *S* and *L*
Totals	1350	678	715	1231	

Linkage on male side 1·9 : 1, *or* 34·5 % *of cross-overs*

$\frac{BG}{bg}$ selfed

	BG	*Bg*	*bG*	*bg*	
	1691	491	421	324	
	62	14	9	8	involving also *S*
	413	92	110	80	„ *L*
	304	67	66	58	„ *S* and *L*
Totals	2470	664	606	470	
Expectation	*2578·9*	*578·4*	*578·4*	*474·1*	

Calculated on {♀ *linkage* 2·2 : 1. ♂ „ 1·9 : 1.

$\frac{Bg}{bG}$ selfed

	BG	*Bg*	*bG*	*bg*	
	1332	488	553	100	involving *S* and *L*
Expectation	*1303·1*	*551·6*	*551·6*	*66·6*	

Repulsion calculated as above

Data for linkage BL

♀ $\frac{BL}{bl}$ × *bl*

	BL	*Bl*	*bL*	*bl*	
	238	124	149	275	
	105	71	64	123	involving also *S*
	197	98	119	169	„ *G*
	97	50	47	96	„ *S* and *G*
Totals	637	343	379	663	

Linkage on female side 1·8 : 1, *or* 35·6 % *of cross-overs*

♀ *bl* × $\frac{BL}{bl}$

	BL	*Bl*	*bL*	*bl*	
	50	31	28	52	
	92	63	53	87	involving also *G*
	423	241	237	411	„ *S* and *G*
Totals	565	335	318	550	

Linkage on male side 1·7 : 1, *or* 37 % *of cross-overs*

$\frac{BL}{bl}$ selfed

	BL	*Bl*	*bL*	*bl*	
	94	35	37	12	involving also *S*
	42	10	10	6	„ *G*
	1462	403	452	243	„ *S* and *G*
Totals	1598	448	499	261	
Expectation	*1686·9*	*417·5*	*417·5*	*283·9*	

Calculated on {♀ *linkage* 1·8 : 1. ♂ „ 1·7 : 1.

$\frac{Bl}{bL}$ selfed

	BL	*Bl*	*bL*	*bl*	
	286	85	113	11	involving also *S* and *G*
Expectation	*263·7*	*107·3*	*107·3*	*16·4*	

Repulsion calculated as above

Data for linkage GL

♀ $\frac{GL}{gl}$ × *gl*

	GL	*Gl*	*gL*	*gl*	
	276	6	12	269	
	305	11	9	258	involving also *B*
	139	4	5	142	„ *S* and *B*
Totals	720	21	26	669	

Linkage on female side 29·6 : 1, *or* 3·2 % *of cross-overs*

♀ *gl* × $\frac{GL}{gl}$

	GL	*Gl*	*gL*	*gl*	
	254	8	4	208	
	142	4	3	146	involving also *B*
	647	7	13	645	„ *S* and *B*
Totals	1043	19	20	999	

Linkage on male side 52·4 : 1, *or* 1·8 % *of cross-overs*

$\frac{Gl}{gL}$ selfed

	GL	*Gl*	*gL*	*gl*	
	986	499	418	—	
	1809	828	851	—	involving also *B*, or *S* and *B*
Totals	2795	1327	1269	—	
Expectation	*2696·2*	*1348·2*	*1348·2*	*0·8*	

Repulsion calculated on {♀ *linkage* 29·6 : 1. ♂ „ 52·4 : 1.}

The tabulations given above include all the numbers bearing on the linkage actually observed. In the following tables the same families, in so far as they are applicable, are arranged for the calculations of linkages between the same factors, *S*, *B*, *G*, *L*, separately for the combinations of any three of them taken together, and collectively for all four. All the expectations are calculated on the linkages determined above, by the application of Trow's method.

♀ $\frac{SBG}{sbg} \times sbg$

	SBG	*sbg*	*SBg*	*sbG*	*Sbg*	*sBG*	*SbG*	*sBg*
	960	977	402	427	85	65	27	27
Expectation	*943·3*		*428·8*		*77·3*		*35·15*	

♀ $sbg \times \frac{SBG}{sbg}$

	SBG	*sbg*	*SBg*	*sbG*	*Sbg*	*sBG*	*SbG*	*sBg*
	870	771	475	444	119	137	54	51
Expectation	*837·2*		*440·6*		*119·6*		*62·9*	

$\frac{SBG}{sbg}$ selfed

	SBG	*sbg*	*SBg*	*sbG*	*Sbg*	*sBG*	*SbG*	*sBg*
	340	49	78	68	6	21	8	3
Expectation	*329·2*	*52·1*	*72·6*	*63·6*	*12·3*	*21·4*	*15*	*6*

$\frac{SBg}{sbG}$ selfed

	SBG	*sbg*	*SBg*	*sbG*	*Sbg*	*sBG*	*SbG*	*sBg*
	1249	85	460	483	15	83	70	28
Expectation	*1210·1*	*53·8*	*529·9*	*445·5*	*12·4*	*91·2*	*105·4*	*26·9*

♀ $\frac{SBL}{sbl} \times sbl$

	SBL	*sbl*	*SBl*	*sbL*	*Sbl*	*sBL*	*SbL*	*sBl*
	177	189	110	100	20	25	9	11
Expectation	*190·4*		*105·7*		*15·6*		*8·7*	

♀ $sbl \times \frac{SBL}{sbl}$

	SBL	*sbl*	*SBl*	*sbL*	*Sbl*	*sBL*	*SbL*	*sBl*
	366	361	215	216	50	57	21	26
Expectation	*361·4*		*212·6*		*51·6*		*30·4*	

$\frac{SBL}{sbl}$ selfed

	SBL	*sbl*	*SBl*	*sbL*	*Sbl*	*sBL*	*SbL*	*sBl*
	1465	211	370	388	26	90	67	23
Expectation	*1489·2*	*216·1*	*364·2*	*317·8*	*51·1*	*97·5*	*75·2*	*28·8*

♀ $\frac{BGL}{bgl} \times bgl$

	BGL	*bgl*	*BGl*	*bgL*	*Bgl*	*bGL*	*BgL*	*bGl*
	289	264	12	11	136	155	5	1
Expectation	*290·4*		*9·8*		*131·7*		*4·5*	

♀ $bgl \times \frac{BGL}{bgl}$

	BGL	*bgl*	*BGl*	*bgL*	*Bgl*	*bGL*	*BgL*	*bGl*
	511	495	8	12	296	278	4	3
Expectation	*516·5*		*9·8*		*271·9*		*5·2*	

♀ $\frac{SBGL}{sbgl} \times sbgl$

	SBGL	*sbgl*	*SBGl*	*sbgL*	*Sbgl*	*sBGL*	*SBgl*	*sbGL*
	86	85	3	3	11	9	44	42
Expectation	*89*		*3*		*7·3*		*40·4*	
	SBgL	*sbGl*	*SbgL*	*sBGl*	*SbGL*	*sBgl*	*SbGl*	*sBgL*
	2	—	—	1	2	2	—	—
Expectation	*1·4*		*0·2*		*3·3*		*0·1*	

♀ $sbgl \times \frac{SBGL}{sbgl}$

	SBGL	*sbgl*	*SBGl*	*sbgL*	*Sbgl*	*sBGL*	*SBgl*	*sbGL*
	362	359	4	9	49	57	211	207
Expectation	*368·6*		*7*		*52·7*		*194*	
	SBgL	*sbGl*	*SbgL*	*sBGl*	*SbGL*	*sBgl*	*SbGl*	*sBgL*
	4	2	—	—	21	26	1	—
Expectation	*3·7*		*1*		*27·7*		*0·5*	

In view of the various combinations involved in the parental constitutions, the results of self-fertilisations in the case of the four factors taken together could only be adequately set out at great length, which in proportion to the information they would add appears superfluous.

Second Linkage Group

Factors involved:

F, flat leaf in the absence of which the margin is crimped (*f*).

Ch, *sinensis*-shaped corolla and calyx many-toothed, usually 10 } in the absence of which { the corolla is *stellata* (*star*) and calyx 5-toothed (*ch*).

♀ $\frac{F\,Ch}{f\,ch} \times f\,ch$ and reciprocal

F Ch	*F ch*	*f Ch*	*f ch*
762	86	72	606

Linkage 8·6 : 1, *or* 10·4 % *of cross-overs*

$\frac{F\,Ch}{f\,ch}$ selfed

	F Ch	*F ch*	*f Ch*	*f ch*
	1404	90	83	383
Expectation	*1374*	*96·8*	*96·8*	*393·5*
	Calculated on linkage 8·6			

$\frac{F\,ch}{f\,Ch}$ selfed

	F Ch	*F ch*	*f Ch*	*f ch*
	514	268	187	6
Expectation	*489·2*	*241·7*	*241·7*	*2·6*
	Repulsion calculated as above			

DESCRIPTION OF PLATES

The drawings reproduced in these Plates were made by Mr C. H. Osterstock.

PLATE XVII

Fig. 1. The deep red stems and leaf-backs formed in the absence of factor *L*.

Fig. 2. The light red corresponding parts showing inhibition of colour due to the presence of *L*.

PLATE XVIII

Fig. 3. Semi-diagrammatic representation of epidermis of petal of a blue flower (*B*).

Fig. 4. Ditto of slaty flower (*b*).

Fig. 5. "Czar." A blue with coloured stigma, on light red stem (*BgL*).

Fig. 6. Slaty, coloured stigma, on light red stem (*bgL*).

Fig. 7. Blue, like Czar, but on dark stem (*Bgl*).

Fig. 8. Slaty, otherwise like Fig. 7 (*bgl*).

Fig. 9. Lee's crimp; *stellata*; single; genetically red. Calyx below.

Fig. 10. Lee's crimp; *sinensis*; single; magenta. Calyx below.

Fig. 11. Lee's crimp; *stellata*; single; P.Q. eye. Colour not determinable without breeding tests.

PLATE XIX

Fig. 12. "Etna." Red, red stigma, dark leaf (*Rgl*).

Fig. 13. A red, corresponding to Etna, with dark leaf, but having the stigma and gynœcium green (*RGl*).

Fig. 14. "Harlequin." *Sinensis* shape.

Fig. 15. "Harlequin." *Stellata* shape.

Fig. 16. Mosaic flower: most of the petals *BRG*, the stripe being *bRg*. Eye P.Q.

Fig. 17. Corresponding uniform flower *BRG*. Eye P.Q.

Fig. 18. A flower uniformly of the same type as the stripe in Fig. 16, viz. *bRg*. Eye P.Q.

Fig. 19. Leaf of *sinensis*, P.Q. eye, crimped, ageing; showing great development of marginal points. The purple colour is exclusively on the lower surface.

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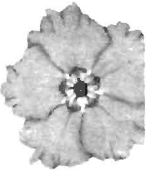

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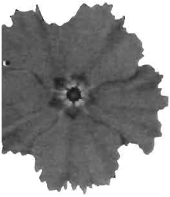
PLATE XIX



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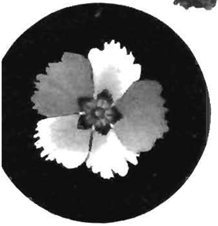

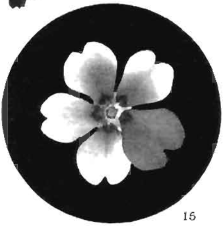

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Fig. 20.

Fig. 21.

Plate XXI

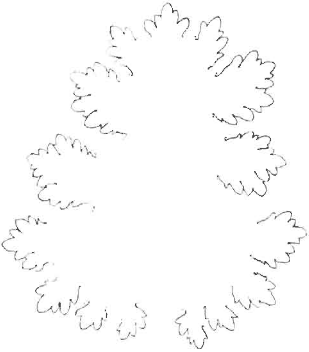


Fig. 24.

Fig. 25.

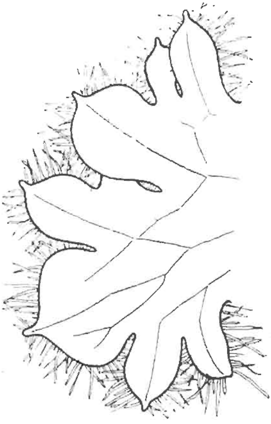


Fig. 26.

Fig. 27.

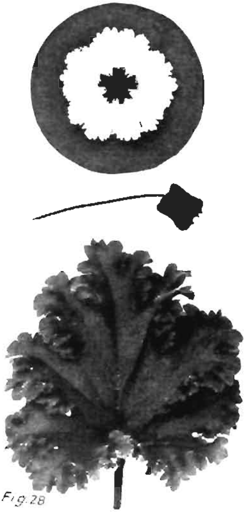


Fig. 28

Fig 29

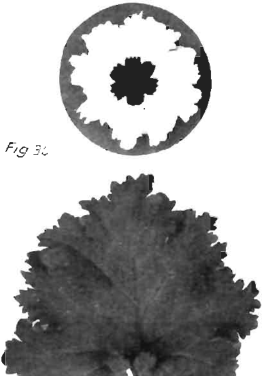


Fig 30

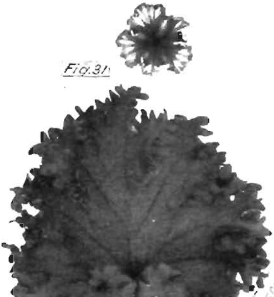
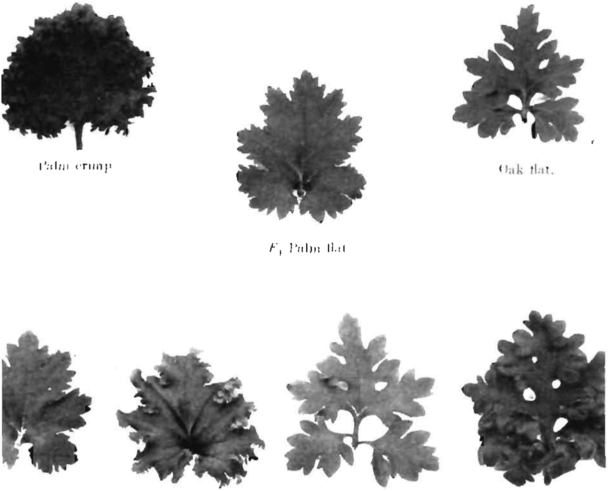


Fig. 31



Palm crimp. F_1 Palm flat. Oak flat.

Palm flat. F_2 Palm crimp. F_2 Oak flat. F_2 Oak crimp.

Fig. 32.

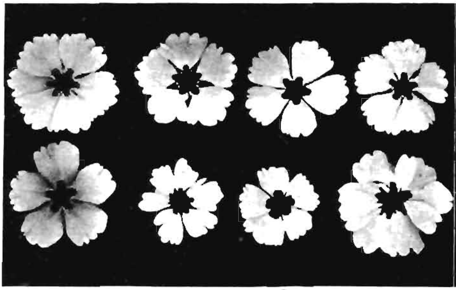


Fig. 33

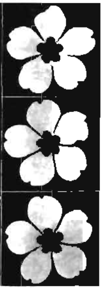
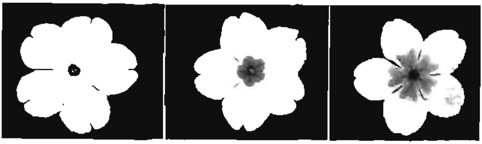
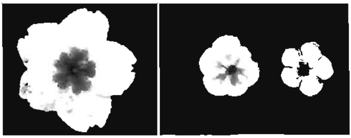


Fig. 34



A. White Alex. B. Normal on flat leaf. C. Pr. Queen on flat leaf.



D. Normal on crimp leaf. E. Pr. Queen on crimp leaf.

Fig. 35.

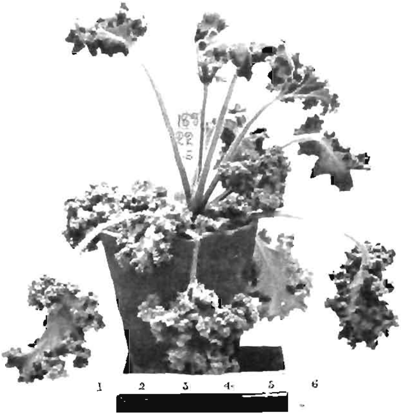


PLATE XX

Fig. 20. Flat Palm.
Fig. 21. Flat Fern.
Fig. 22. Flat Oak.
Fig. 23. Flat Fern Oak.

PLATE XXI

Fig. 24. Palm leaf, flat. Outline of margin divided to avoid imbrication.
Fig. 25. Oak leaf, flat. Outline of margin.
Fig. 26. Palm crimp, *stellata*. Outline of portion of margin magnified.
Fig. 27. Palm crimp, *sinensis*. Outline of portion of margin magnified.

PLATE XXII

Fig. 28. Lee's crimp, *stellata*. Leaf, calyx, and flower.
Fig. 29. Lee's crimp, *sinensis*. Leaf, calyx, and flower.
Fig. 30. Sutton's crimp, *sinensis*. The low degree of crimping.
Fig. 31. Sutton's crimp, *sinensis*. In combination with P.Q. eye, showing increase in crimping and malformation of flower as usual in this combination.

PLATE XXIII

Fig. 32. Palm crimp × Oak flat, with F_1 and the four combinations in F_2.
Fig. 33. Flowers from oak-leaved plant, *sinensis*, showing peculiar shapes common in this combination.
Fig. 34. Corresponding *stellata* flowers; petals narrow but not malformed.

PLATE XXIV

Fig. 35. Various Eyes.
- A. White or "Queen Alexandra."
- B. Normal on flat leaf.
- C. "Primrose Queen" (P.Q.) eye on flat leaf.
- D. Normal on Lee's crimp leaf: fringe here abnormally weak.
- E. P.Q. on crimp leaf.

Fig. 36. Plant of crimp type combined with *sinensis* flowers as seen in July, with proliferation of crimping.

SOMATIC SEGREGATION IN PLANTS

[*Report of the International Horticultural Congress held at Amsterdam, Sept.* 17—23, 1923]

RECOGNISING that the view, developed especially by Morgan and the American school, that the segregation of Mendelian elements is effected in the process of maturation of germ cells, must be in great measure correct, he called attention to evidence which strongly suggested that in plants at least segregation might not very uncommonly occur at other stages of the life-history. He gave illustrations especially from *Bouvardia* and *Pelargonium*, showing that propagation by roots produced in certain kinds and sometimes with much consistency, varieties quite distinct from the parent plants. Plants which have this property must be regarded as chimæras, and in some examples at least the chimæra must be periclinal, by which is meant that the outer layers of the plant are in constitution distinct from the inner core. When shoots are made to arise from roots, the nature of this inner core is manifested.

This distinction between the outer and inner parts must be imagined as having occurred at some very early stage in the history of the plant, probably during embryonic development.

Question next arose whether the "bud sports" so frequently seen in practical horticulture, resulting often in the production of a novelty (as in *Chrysanthemum*, Carnations, etc.) ought not for the most part to be regarded as evidences of an (*original*) mosaic nature rather than of a contemporary variation.

In this connection attention was called to the remarkable fact that when colours were distributed in certain patterns, the plant might regularly bear flowers of the same pattern, and be bred true, whereas if the same colours were arranged on a different geometrical plan, neither would the flowers of a single plant be consistently uniform, nor would the seed come true to the pattern. He contrasted for instance picotee carnations with bizarres. Picotee, in which the colour is in the edge of the petals, is a stable arrangement, but bizarre, in which the colours are in wedge-shaped stripes, is not, though the pigments involved may be the same.

Photographs illustrating this phenomenon in *Tagetes* were shown. In the variety "Legion of Honour" the base of each floret is brown on

a yellow ground. The florets collectively thus give a ring of brown surrounded by a ring of yellow. The variety "Star of India" shows a different arrangement of the same colours. In it the pattern regarded as the type of the variety consists of florets each having a stripe of brown on the outside petals, the central area of the floret being yellow. The florets together thus compose a head like a star with brown and yellow rays. Messrs Sutton, to whom the speaker was indebted for an introduction to this curious example, found that though Legion of Honour varies very little and breeds practically true, the heads of Star of India are continually subject to extreme irregularity, the flowers of one plant differing enormously among themselves in the amount of brown, many being wholly yellow and others patched in asymmetrical and irregular ways. It has been found impossible to breed this variety even approximately true to the chosen type.

Similar examples occur in *Dahlia*, *e.g.* Helvetia known in England as Union Jack which has a red stripe on the outsides of the florets, thus agreeing with *Tagetes* Star of India.

These phenomena pointed to distinctions in the geometrical or mechanical control of somatic segregation, but no analysis of its nature could as yet be attempted.

The speaker hoped that practical horticulturists who witnessed analogous occurrences would make their experiences known, for they might not improbably give important clues to the geneticist.

NOTE ON THE NATURE OF PLANT-CHIMÆRAS

(With Plate XXV)

[*Studia Mendeliana*, 1923]

SINCE Baur first pointed out the interest of the subject, plant-chimæras have attracted the general attention of geneticists. We are agreed that in the chimæra we find commonly, if not always, a mosaic of parts differing not only in their visible characters but in their genetical properties also. Whether the segregation which results in this collocation of genetically distinct parts is determined in embryonic divisions or at some other stage before or subsequent to them we cannot say, but the consequence is that the plant-chimæra is a mosaic of two or more parts which behave genetically as if they were distinct organisms. As Baur showed, when the distribution of the two is of the periclinal kind, the one forming the core, the other the outside including the subepidermal layer, the germ cells have the properties of that which provides the outside. When the distribution is sectorial, the inheritance is irregular and the mixture which results can be regarded as consisting of contributions from both ingredient members.

Upon this simple foundation many complexities ensue which have been only partially elucidated. When for example the ingredients of the sectorial chimæra are finely divided, the intimate mixture may breed with much constancy as if it were an individual genetic whole, as for example may be seen in a race of *Primula sinensis* formerly largely grown by Messrs Sutton, which rarely gave any self-coloured plants. Similar examples occur in *Antirrhinum* and *Mirabilis*, and when Mendelian analyses were first attempted, the interpretation of these mosaic plants was a matter of much difficulty, and many mistakes were made. From analogy with animals the mosaic was regarded as a recessive to the self-colour, as the Dutch rabbit is. In general it might breed true, or throw also the pure recessive, which is consistent with that representation; but difficulty arose inasmuch as even fine mosaics might occasionally throw the dominant self-colour.

The analogy with animals is however probably inadmissible. Animals mosaic in sex and in characters dependent on sex are well known, but as to other real chimæras in animals there is little certain warrant. For a plant with a parti-coloured flower to breed true like the Dutch rabbit, the parti-colouring must be arranged in a definite

and consistent pattern, as that of a picotee carnation is. Such a parti-colouring distributed on a regular geometrical plan, can breed true; but when the same colours are grouped in a disorderly way, as those of the bizarre carnations are, they are liable to throw self-coloured dominants.

In terms of presence-and-absence the facts are readily expressed, and though we cannot yet define the geometrical distinction between the two classes of patterns, we can generally recognise it.

In the intimate mosaic the gametes transmitting the mosaicism must be regarded as themselves mosaic, containing less than the whole of either factor. Such gametes can enter into heterozygous combination with gametes bearing either of the self-colours (whether dominant or recessive). That this is a correct representation is not doubtful, though we have as yet no clear conception of the cytological process involved.

Mosaicism may be of many degrees of coarseness or fineness, according to the special type or character concerned. Whether somatic cells may be themselves mosaic is uncertain, but not rarely small groups of cells, or even single cells may show one or other of the characters and be surrounded with other cells bearing the opposite. When from mosaics larger parts arise, wholly of one or other character, we have no difficulty in supposing that the growing point, or other original rudiment (*Anlage*) from which they were developed, was such a cell possessing the character in its integrity.

It must not be expected that germ cells derived from the several parts will be true to their character, since (1) these parts may be heterozygous in respect of the mosaic condition; and (2) the underlying germ cells need not necessarily have arisen from the same rudiment as the somatic part in which they occur.

In the main this method of representation is a sound guide. The fact that the offspring of self-fertilised periclinals reproduce the characters of the subepidermal layer, whether white or green respectively, has been now frequently confirmed, and has been often witnessed in the work of this Institution on plants of various kinds.

In an important paper Noack[1], from microscopical examination of the processes of growth, has been led to question Baur's view. Both outer and inner parts, according to his observations, are formed by differentiation from the same subepidermal cells. The distinction between the two is not determined once for all, but is a continually

[1] Pringsheim's *Jahrb. Wiss. Bot.* LXI, 1922, p. 459.

recurring process. How the observations of Noack are to be reconciled with the fact that the genetical properties of the plant are with much consistency those of the subepidermal layer is as yet unknown.

In our experience with these periclinal chimæras we have, in three several varieties of Zonal Pelargoniums, seen an occurrence which must be taken into consideration in further attempts to interpret the, phenomena. Caroline Schmidt is a well-known zonal, with crimson-red double flowers; and with foliage white-over-green, scarcely distinguishable from that of the type used by Baur in his original experiment. Like most periclinals this variety is liable to throw up shoots, presumably from the core, in this case wholly green. Our expectation would be that these shoots would remain green in perpetuity. We imagine them coming out clean from the outer coat. Nevertheless a plant propagated from such a green shoot, which planted out in open ground had made much growth, developed white-over-green parts at some height from the ground. These were first noticed as occasional patches of white on leaves like those seen in Fig. 2, but later, owing obviously to the change involving the apex of a terminal growing point, a whole shoot arose, white-over-green, exactly reproducing the original Caroline Schmidt. This has remained so ever since.

Flower of Spring, a white double-flowered form, behaved in a similar way. This variety is also white-over-green, but is peculiar in the fact that at some stages of growth the white has a greenish tinge. One of the solid green stems which it produced bore from its base the shoot shown in Fig. 2. White patches partially overlying the green are visible in several leaves. The change here has not so far involved the apex of the growing plant.

Lastly, the same behaviour bas been seen in the case of the white-over-green variety, with scarlet single flowers, originally used by Baur in his own experiment. Many years ago he very kindly gave me cuttings of his plants which we have grown and frequently propagated here. The white-over-green form put up green stems from its base, as such plants commonly do, and one of these has produced, again from its own base, a shoot with a white periclinal coat exactly as in the original parent variety. This shoot is in appearance like that shown in Fig. 1, but the plant there photographed is somewhat unusual in the fact that the "sport" in it came high on the plant and not from the base.

When tbe first of these returns to the periclinal chimæra appeared,

Fig. 1.

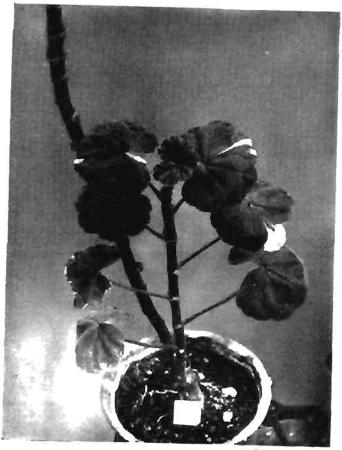


Fig. 2.

we interpreted it as showing that even in the green core there must have been an "island" of albino tissue which eventually came to the surface. Such an account may be correct; but inasmuch as the return has happened three times in green plants derived from as many distinct varieties, we have then to suppose that islands of albino tissue are in such plants common. Alternatively we may imagine that in Pelargoniums of this class loss of green plastids is a frequent possibility; but since green zonals in general are by no means subject to this variation, the liability must be attributed especially to the cores of periclinals, a suggestion which imperils the simplicity of the original interpretation.

DESCRIPTION OF PLATE XXV

Fig. 1. Return of white periclinal tissue in green plant derived from the core of Caroline Schmidt.

Fig. 2. Flower of Spring showing the same phenomenon (the tall stem at the back, from the base of which the young shoot arises, is wholly green).

DR KAMMERER'S ALYTES

[*Nature*, CXI, 1923]

THOSE who have followed the discussion of Dr Kammerer's claims will be aware that special interest has centred on the questior whether he could produce for examination males of Alytes showing the modification alleged to occur in consequence of his treatment. Some of the circumstances which aroused scepticism are related in my letter to *Nature*, July 3rd, 1919, p. 344[1]. We were originally told (*Arch. Entwm.*, 1909) that nuptial callosities or *Brunftschwielen* appeared on the thumbs of males of the treated strain, and that in the 5th treated generation (Kammerer's F_4) *all* the males had these structures. They are a conspicuous feature in most Batrachia, and Alytes is one of the few forms in which they are not known to occur. Since normal Alytes mate on land and the treated animals were made to pair in the water, we were asked (1909, pp. 516–7) to see in these *Schwielen* a true functional adaptation. The rugosities were developed to give the males a better grip of the slimy females.

Dr Kammerer remarks that any one who has compared the feel of a dry toad with that of a wet one will not question that rugosities on those parts of the limb which come into contact with the body of the female are a very necessary equipment for an aquatic embrace (p. 516). This theme was developed at considerable length. In *Arch. Entwm.* 1919, the same argument reappears, and, various other hypotheses being discussed and set aside, it is argued that the most probable cause of the development of rugosities was to be found in the change of mating habits. The process of mating in the water takes twice or thrice as long and is far more laborious. If his interpretation is right, Dr Kammerer continues, the development is to be regarded as a "*funktionelle Anpassung*: ihre nachweisliche Erblichkeit würde hierdurch an theoretischer Tragweite gewinnen" (p. 339).

Up to 1919 nothing but vague diagrams (1909, Figs. 26 and 26 *a*) had been offered us to show what these new organs looked like, and no detailed description had appeared. Dr Kammerer in that year published the long paper mentioned above, making some new statements which I will consider presently. In illustration a photograph of the whole animal (F_5 in 1913) was given. This picture was rather like those handed about a few years ago as "spirit-photographs,"

[1] [See this vol., p. 272.]

and for demonstrational purposes was worthless. There were also several drawings, and a photograph, representing sections through the skin of a supposed *Schwiele*. At about that time Dr Przibram was good enough to send me a slide with six similar sections labelled "F_3," which I have shown to numerous colleagues. As regards the sections and representations of sections, I do not question that they may have been taken through real incipient rugosities, but the development is slight and ambiguous.

The description of 1919 amplifies that of ten years before. The rugosities were originally described as in the proper place, namely, on the upper (sc. dorsal) and radial surface of the thumb; and as more males of F_4 and F_5 came into breeding condition, rugosities appeared not simply on the bases of the thumbs but extended in various degrees and with individual differences up the inside of the forearm. Inasmuch as various Batrachians have rugosities in that region (showing also individual differences and asymmetries), and since in the embrace of Alytes the parts named are in contact with the female, the new account raised no fresh improbability—rather the contrary. Many modified males are said to have been under Dr Kammerer's observation during three years after he had (1910) been challenged to produce one, but a photograph of a single specimen —and that absolutely non-committal—was all that had been published to show the structures in position. We are told that the 1913-hatched brood failed to breed, and the last male (F_6) died in 1914 (1919, p. 328).

But one specimen (presumably that photographed) was known to be preserved in Vienna. It had been examined by visitors to the Versuchsanstalt, who reported verbally and variously as to what they had seen. A few weeks ago the announcement was made that this Alytes would be shown in Cambridge, and I received an invitation to attend a meeting at which it would be exhibited. Knowing that Dr Kammerer had abstained from appearing at the Congress of geneticists which met at Vienna in September last, I inferred that he had no new evidence to produce, and I therefore excused myself from attendance, not wishing to enter deliberately into what was likely to prove a profitless altercation. When, however, an exhibition before the Linnean Society was arranged, I naturally attended as a fellow of the Society to see what I could. I expected to see a dark mark on the thumb or other fingers extending perhaps more or less over the wrist or up the forearm; and whether this was to be inter-

preted as a nuptial rugosity or *not*, would, I imagined, be more or less a matter of opinion.

What I did see was something altogether different. The animal was fastened with its back against an opaque plate in a cylindrical museum glass, with the ventral surface exposed. The right hand showed nothing special, but *across the palm* of the left hand was a broad dark mark. It looked like a piece of thickened, blackish-brown skin. Examining it with a good lens I could see no papillary or thorny structure, though considering the minuteness of the alleged spines, I scarcely expected to make them out very distinctly. But the appearance was quite unlike that of any natural *Brunftschwielen*. In them, even in *Rana agilis* which has them developed very slightly, one sees with a lens characteristic grey specks, not a dark uniform surface as in the creature exhibited. I do not mean that there was no break in the pad as a whole, about which my memory is doubtful, but that the surface was uniform and the colour continuous in tone, without the dotting or stippling so obvious in true *Brunftschwielen*. That there was no development on the right hand was explained. The skin had been snipped off during life to furnish sections.

A photograph of the palm of a hand was thrown on the screen. This palm was pointed to as showing rugosities, but I saw none. In the specimen exhibited, the backs of the digits were not visible, nor were we shown any photograph of them.

I direct attention first to the fact that the structure shown did not look like a real *Brunftschwiele*. Next I lay stress on its extraordinary position. *It was in the wrong place*. Commenting on the evidence, I pointed this out. In the embrace of Batrachians the palms of the hands of the male are not in contact with the female. Those who looked at the specimen naturally concluded that they must be. One speaker confidently told me in the discussion that I was wrong, and that in the common toad the rugosities *are* on the palmar surface! To show how the hands are placed I send a photograph (Fig. 1)[1] of a pair of *Rana agilis* killed and preserved while coupled. The lower digits of the male's hands are the thumbs.

Clearly the rugosities, to be effective, must be on the backs and radial sides of the digits, round the base of the thumb, as in our common frog, on the inner sides of the forearms, or in certain other positions, but not on the palms of the hands. There are, of course,

[1] [This figure has not been reproduced, as the block published in *Nature* was unsatisfactory and the original is no longer available. ED.]

minor variations, in correspondence with which the positions of the rugosities differ. The clasp of Alytes, for example, is first inguinal and afterwards round the base of the head (Boulenger). Minute thorns may be formed on the back of Bombinator and perhaps in other places on the skins of Batrachians, where they cannot serve as *Brunftschwielen*; but on the palm of Alytes they would be as unexpected as a growth of hair on the palm of a man.

Dr Kammerer's own reply was on different lines from that of the speaker I have mentioned, but curious and, as I thought, significant. He asked us to note that in his lecture he had refrained from using the word "Adaptation"—a defence sound perhaps, though surely disquieting to his disciples.

The discoveries claimed by Dr Kammerer are many and extensive. To geneticists that regarding heredity and segregation in Alytes (*Verh. naturf. Ver. Brünn*, 1911) which I called in question at the Linnean meeting is the most astounding. But what I then heard and saw strengthens me in the opinion expressed in 1913, that until his alleged observations of *Brunftschwielen* in Alytes have been clearly demonstrated and confirmed, we are absolved from basing broad conclusions on his testimony.

Dr Kammerer's Alytes

[*Nature*, cxi, 1923]

Professor MacBride's letter in *Nature* of June 23rd, p. 841, did not at first seem to require any rejoinder. But I find that some botanists, and perhaps others unfamiliar with zoological terms, suppose that the quotations from Boulenger contradict my statement that rugosities are not formed on the palmar surfaces. Boulenger, of course with perfect accuracy, states that rugosities in various genera appear on the *inner* side of the digits (italicised by Professor MacBride). This is the *radial* side, as emphasised in both our letters, not the palmar surface, which was the part which bore the extraordinary structure visible in Dr Kammerer's specimen.

[*Note.* For the further development of this controversy see *Nature*, cxviii, 1926, pp. 209, 264, 578, 661. Ed.]

ON CERTAIN ABERRATIONS OF THE RED-LEGGED PARTRIDGES *ALECTORIS RUFA* AND *SAXATILIS*

(With Plates XXVI—XXIX)

[*Journal of Genetics*, XVI, 1925]

INTRODUCTION

IN 1923 Mr P. R. Lowe, Assistant Keeper in the British Museum Bird Room, brought to my notice two very striking and quite distinct aberrations of the Red-legged Partridge (*Alectoris rufa rufa*) which the Museum possessed. The first, which we call the "bright" variety, was represented by three specimens which all came from localities not very far removed from each other in the west of England; and of the second, which we call the "dull" variety, there were also in the collection three specimens, two from Kent, having been shot in the same field in successive years, and a third from Essex. Subsequently we came to know of another specimen sent by Lord Deerhurst to Rowland Ward's for mounting, which though presenting certain differences agreed in many respects with the "bright" birds. On hearing of the interest attaching to it Lord Deerhurst very kindly presented the bird to the Museum. We learnt also from him that the bird was one of several similar birds which had been observed in his neighbourhood during a period of years. This locality (Pirton in Worcestershire) is moreover not far from those of the other "bright" birds.

Exact details respecting the origin of the several specimens of both varieties are given below.

Briefly the distinguishing features of the "bright" variety as represented by the first three specimens (Lord Deerhurst's bird being for the present omitted from consideration) are as follows:

1. Head *black*, not reddish brown.
2. Feathers of mantle, scapulars and wing coverts in various degrees *barred*, in such a way that many of them repeat the chevron marks so conspicuous in the flank feathers of the normal.
3. Tail coverts *bright chestnut brown* like the normal rectrices.
4. Whereas the normal has the throat a clear white, limited posteriorly by a solid black band or "gorget," in the bright variety

this sharp differentiation is diminished, and the throat is a dingy grey, with a thin band of broken colour in the place of the gorget.

Lord Deerhurst's bird differs from the three bright birds in being much paler in colour, and in the fact that the head is *not black*, but as regards the features numbered 2, 3 and 4 it agrees with them fairly well. This bird is evidently immature, and with some probability its special peculiarities may be ascribed to juvenility.

The characteristics of the "dull" variety are:

1. The *throat* is *black*.

2. The *chevron marks* of the normal flank feathers *are altogether absent*.

3. The *rectrices* are not chestnut brown as in the normal but are of the same *dull colour* as the tail coverts.

4. The dorsal plumage is much as in the normal, except that the feathers of the neck are little differentiated; but the ventral surface is altogether peculiar, being, except for the black throat, of a more or less unicolourous brown. This brown is reddish anteriorly on the part of the breast which in the normal is ashy blue. The flanks and belly are a dull brown, broken by a central patch of irregularly-placed white feathers just posterior to the breast.

Minor distinctions will be specified in the detailed descriptions.

So far as we are aware the only published reference[1] to either of these varieties of *A. rufa* is a brief account given of the "bright" variety by Mr Lowe in the *Field*, 15 March, 1923, illustrated with a black and white sketch by Mr Frohawk.

From a mention by Ogilvie-Grant[2] we learned however that Fatio had recorded a variety of another species, *A. saxatilis*, as characterised by *a black head*, which is so conspicuous a feature of our bright variety. A description of two specimens showing this feature was published by Fatio[3] with a black and white plate showing the general appearance of the variety and a plate in colour giving representations of a number of feathers. Obviously the variety *melanocephala* strongly resembles our bright birds. As these birds had been presented to the museums of Sion and Bex my son went to Switzerland to examine them in detail, which by the courtesy of the curators he was permitted to do. He was also successful in finding in the

[1] For earlier references see note at end of the paper.

[2] F. M. Ogilvie-Grant, *Handbook to the Game-Birds*, I, 1895, p. 91. Allen's Naturalists' Library. Ed. R. Bowdler Sharpe.

[3] V. Fatio, "*Perdix saxatilis* var. *melanocephala*: curieux déplacements de Couleurs." *Mém. Soc. Zool. France*, VII, 1894, p. 393.

Geneva Museum another specimen of *A. saxatilis* which though approximately normal had a few of the abnormal barred feathers in the scapular region. He has prepared the following account of the whole series, including our three bright birds, Lord Deerhurst's bird, the three dull birds—all *Alectoris rufa rufa*; the two bright birds at *Sion and Bex respectively, the peculiar specimen at Geneva—all Alectoris saxatilis*; together with observations made on a considerable number of birds of both species which may be regarded as normal.

If scientific names are required for the designation of these aberrations we should follow Fatio in referring to the bright variety in both species as var. *melanocephala*, and to the dull birds we may give the name var. *obliterata*.

Description of Material

List of Specimens.

Alectoris rufa rufa var. *obliterata*

(Fig. A, Plates XXVI and XXVII)

This form, which is referred to as the "dull" variety, is represented by three specimens, all of which are in the British Museum. Their data are:

(1) ♂, *from* Spaynes Hall, Braintree, Essex; *shot* 20 Oct. 1908. Presented by A. W. Ruggles Brise, Esq. Pls. XXVI and XXVII, A. Reg. No. 1908 . 10 . 22 . 1.

(2) ♂, from Higham, near Gravesend, Kent; shot 1 Sept. 1914. Presented by Dr Hammond Smith. Reg. No. 1915 . 1 . 15 . 1.

(3) ♂, from Mockbeggar, Rochester; shot 1 Sept. 1915. Presented by Herbert Cobb, Esq. Reg. No. 1915 . 10 . 5 . 1.

The label states that (3) was shot in the same field as (2). This is as a matter of fact in accord with the names of the locality, which may well be synonymous.

As far as we know, no other specimens of the var. *obliterata* have been seen.

Alectoris rufa rufa var. *melanocephala*

This form is generally referred to in the paper as the "bright" variety. There are four specimens in the possession of the British Museum. Their data are:

(1) ♂, from Overbury, Worcestershire (near Bredon Hill); shot 9 Oct. 1903.

Presented by Wynyard Warner, Esq.

Reg. No. 1904 . 10 . 2 . 1. Figured by Lowe, *Field.*

(2) Old ♂, from Norton Hall, Gloucestershire (near Gloucester); shot 26 Oct. 1922. Pls. XXVI and XXVII, c.

Presented by Major Robert Bruce.

Reg. No. 1923 . 1 . 29 . 1 (genitalia preserved).

(3) From Kinver, near Stourbridge, Worcestershire; without spurs; ? ♀. 1923. [No date.]

Presented by A. H. Guest, Esq.

Reg. No. 1923 . 3 . 11 . 1.

(4) Juvenile ? ♀, from Hermitage Farm, near Pirton Court, Worcester.

Shot 21 Sept. 1923 and presented by Viscount Deerhurst.

This bird differs from the others in numerous points and therefore has been described separately.

Besides these four specimens which are preserved in the British Museum, Lord Deerhurst records that in 1919 a covey of partridges near Pirton Court contained three birds probably all of this type. One of these was shot to pieces but the other two escaped and were never seen again. In 1922 he himself shot a brightly coloured partridge in the same part of the same field as the specimen which he shot a year later and gave to the Museum (No. 4 in the list). Thus in all there are three specimens of the dull birds and four of the bright birds. The three dull birds are all *males* and all from the east of England, the four bright birds are males with the exception of Nos. 3 and 4, which are doubtfully females; all four are from the west of England, where four other similar birds have been seen.

This distribution of the two varieties is remarkable, and since red-legged partridges are so frequently shot there is no doubt that the two varieties are almost confined to the respective areas as we know them.

Alectoris græca saxatilis

No specimens comparable with the dull birds are known. There are three specimens which are comparable with our bright variety of *A. rufa*. These are:

Alectoris græca saxatilis var. *melanocephala* Fatio

(1) Juvenile, 17 November, 1878, shot close to Sion in the Canton de Valais by Alphonse Bonvin, who told Fatio that it was the only

abnormal bird in a covey of eight, five of which were shot. This specimen is now in the Musée de l'École Scientifique at Bex in Valais.

(2) ♀ adult, 11 December, 1879, shot in the Val d'Herens, near Sion, by A. Bonvin. This bird is in the Musée Cantonal at Sion.

(3) A bird in Geneva University Museum which differs from the normal notably in possessing *a few barred dorsal feathers*. It has the following data: No. $\frac{763}{44}$, ♀ Orsières, Valais, November 1912, presented by *M. Ghidini*.

This bird is separately described.

Thus all three of these "bright" birds were taken in the same canton of Switzerland within a radius of thirty miles. (1) and (2) are substantially alike, but (3) approximates to the normal except in the *fact that it has some barred feathers on the back.*

Description of the Forms

Alectoris rufa. "Dull" variety or var. *obliterata*

Dorsal and ventral views of this form are shown in Pls. XXVI and XXVII, A; separate feathers in the bottom row of figures in Pl. XXVIII. The three specimens are all very much alike, and differ strikingly from the normal birds in the loss of all those contrasts of colour which make up the decorated appearance. This is most noticeable in the flank feathers, which, instead of being brightly coloured and ornamental as in the normal (Pl. XXVIII 1, B), are grey at their bases with brownish grey tips (Pl. XXVIII 1, A). Correspondingly the rest of the body is dully and uniformly coloured. The feathers of the breast which are ashy in the normal are tipped with brown, matching the dorsal and flank feathers. The abdominal feathers are similar and only very slightly paler than those of the back.

The tail feathers instead of being chestnut are a dull greyish brown with spots of darker pigment, but otherwise match the tail coverts. This last point is especially worth notice since in the bright variety the coverts and rectrices match, but there the uniformity is brought *about by a change in the colour of the coverts, not of the rectrices as* in the dull birds.

The primary flight feathers are almost normal, possessing still some traces of the pale streak in the normal feathers near the tip. But this streak is much reduced on the more internal primaries and is completely absent from the secondaries.

The only contrasts of colour are provided by the throat and by the

irregular white patches (present on all three birds) on the lower breast. The throat is black and these black feathers are followed by patterned feathers comparable with those on the lower neck of a normal bird but much less conspicuous. The pattern consists of black marks upon a dull brown ground, not on the white and grey ground of the normal. The similarity of the patterns on the neck feathers of the type and the variety, and the fact that in each case these patterned feathers are preceded by a black area, make it appear as if the factors which are responsible for the black area and for the patterned feathers had changed their sphere of influence, producing similar colours more anteriorly on the neck, obscuring the white throat and leaving their old areas to the mixed grey and chestnut pigments which make up the dull brown of the remainder of the bird. On the dorsal side of the neck there are some patterned feathers, which feathers bear the same patterns and occupy approximately the same area as on the normal, but again the pale background has been replaced by dull brown.

Before leaving these birds, for the sake of completeness I should add that specimen No. 1 has a single scapular feather with a black fringe at its tip, and that the same bird has a single abdominal feather much paler than the others—dirty yellow with black markings on it which form an imperfect V of which the point is directed outwards.

Specimens Nos. 2 and 3 have each of them one or two irregular feathers. On one of these birds (Mockbeggar) there is a feather with a brown mottled centre among the feathers of the white patch. Another breast feather of the same bird has an irregular black mark on each side.

Alectoris rufa. "Bright" variety (Pls. XXVI and XXVII, c)

Of the four specimens of this type three are nearly alike; the fourth is very much younger than the others and will be described separately, since some of its juvenile characteristics have a bearing upon the variation of *Alectoris saxatilis.*

The three similar birds have the following characteristics:

The dorsal side of the head (*i.e.* the cap), which in normal birds is greyish brown with very small patches of black hairlike feathers round the base of the bill, is uniformly black. The concealed bases of the feathers are pale grey.

The details of distribution of black pigment in the cap of normal and abnormal birds are perhaps worth noticing:

In the normal there are little hairlike black patches laterally at the base of the bill and smaller patches dorsally and ventrally at its insertion. (These patches are also present in *A. saxatilis*, in which species they are more clearly developed than in *A. rufa*.) They are followed posteriorly by a few feathers with black bases and grey tips; *i.e.* there is an antero-posterior series of feathers on which, as we proceed backwards, the black is seen to be more and more closely confined to the base of the feather, until after a few feathers it is present only as a trace at the base of the feather and finally disappears. This arrangement of pigments is very typical of the colours of feathers, and in this paper we shall speak of it as the *basipetal disappearance* of colour. Another similar case will be described in the black collar band of normal *A. saxatilis*.

In the abnormal birds the arrangement of black pigment is very different. The base of the bill is, as in the normal, surrounded by patches of short black hairlike feathers, but these are succeeded posteriorly by feathers which are greyish white at the *base* and black at the *tip*. Behind these tbe area of the black increases and soon covers the whole feather, until it is displaced by grey which starts at the tip and spreads downwards, covering a larger and larger area as we proceed down the median dorsal line of the neck. In this region the series is complicated by some patterning of which there is no need to give details beyond stating that this patterned region corresponds to a similar larger region on the neck of the normal, where the patterns are substantially the same but more conspicuous on account of the pale grey-and-white ground colour. In the Overbury bird, however, the laced feathers of the gorget are present also dorsally, forming a central band on the back of the neck.

This description of the head holds good for the Norton Hall bright *A. rufa* and for the adult *A. saxatilis*, but in the case of the juvenile *A. saxatilis* and of the Kinver and Overbury birds there are many feathers on the top of the head which are black with a greyish chestnut fringe. This fringe shows little serial change in breadth, and so must be regarded as some form of barring. (Cf. p. 395.)

Turning now to the ventral side, in the normal bird the throat is white, behind it is a heavy black band (gorget) which grades off into patterned grey, black and white feathers. In the bright variety the throat is not white but a dirty pale grey, the heavy black band is

absent and the area of the patterned feathers much reduced. This condition resembles closely that of young normal *A. rufa*, in which the black band does not appear until after the patterned feathers are formed (cf. description of the juvenile bright bird in which absence of black on the head is ascribed to its immaturity).

Though dorsally there was no change in the patterns of the neck feathers, they being apparently simply streaked with a black longitudinal line on each side as in the normal, ventrally there is a considerable change, which is shown in Pl. XXVIII, figs. 8 B and C. In the normal the black is segmented by transverse invasions of greyish white; in fact the feather may be regarded as transversely barred. Proceeding posteriorly in the series the proximal segments of black fade away while fresh segments are separated off from the large black spots at the tip. In the bright variety there is no trace of this segmentation. The feathers have pale yellow centres and black margins. Feathers of this type are also found in the *nuchal* region of the Overbury bird.

The remainder of the ventral side of the bright variety is normal. The flank feathers which are by accident partially hidden in Pl. XXVII C are normal[1], as also are the grey feathers of the breast and the yellow abdominal feathers.

The feathers of the back and wings remain to be described. These are most conveniently considered as in three separate systems:

(*a*) Median dorsal group, extending from the insertion of the neck back to the rectrices. In this group the term "mantle" is used for those feathers which are inserted on the back between the two scapular pteryloses.

(*b*) Scapular feathers.

(*c*) Wing coverts and remiges.

(*a*) *Median dorsal group of feathers.*

Feathers of the mantle are shown in Pl. XXVIII, fig. 4 C and in Pl. XXIX, fig. 3. The more lateral feathers of the group are strongly curved and the barring of the normal flank feathers is very closely reproduced but the pattern has become asymmetrical, giving, instead of a transverse bar, a chevron mark which is best developed on the outer side of the feather. Among these feathers are a few on which the bar

[1] The differences in the flank feathers shown in Pl. XXVIII, figs. 1 B and C, and Pl. XXIX, figs. 5 and 6, are probably due to the feathers having been taken from slightly different parts of the pterylosis.

is apparently doubled—Pl. XXIX, fig. 12. In these a second black bar has appeared proximal to the first and separated from it by the pale bar which is present on normal flank feathers and on the neighbouring mantle feathers. The pattern so arrived at is comparable with that of the normal flank feathers of *A. saxatilis*, on the flanks of which the proximal black bar is always well developed (Pl. XXIX, fig. 10). Occasionally, too, this bar is faintly developed on the extreme anterior flank feathers of normal *A. rufa* (see Pl. XXIX, figs. 13 and 14), so that it is by no means surprising that this bar shows itself in the mantle feathers of the variety.

The more central feathers of the mantle are symmetrical (Pl. XXVIII, fig. 4). They are pale feathers with a broad dark **V** on the fan; outside the **V** is a paler fringe. Behind the mantle on the back the dark mark is broader and blacker (Pl. XXVIII, fig. 5 C) and is on some feathers partially split into two transverse bars by formation of an island of chestnut. But the division never proceeds very far in this region of *A. rufa*.

Following the median dorsal series backwards, apart from the tendency to divide, the bar does not change its position on the feather. It becomes paler on the posterior part of the back and finally fades away in place—it does not disappear basipetally like the black of the head feathers. (See Pl. XXVIII, figs. 4, 5 and 6 C.)

The black still persists as a faint mark near the tip of the rump feathers (so faint that it does not show in Pl. XXVIII, fig. 6 C). But one of these feathers on the Norton Hall bird has a distinct elliptical black line, the long diameter of the ellipse coinciding with the rachis. The centre of this ellipse is filled with chestnut. This feather is quite isolated and no doubt indicates a stage in the development of the broad black bar and its partial splitting.

The tail coverts are almost self-coloured with a darker chestnut tip on a pale chestnut ground. These shade off gradually in colour to the dark chestnut of the rectrices.

In the normal bird, too, the rectrices are chestnnt, in marked discontinuity with the grey of the rump feathers and tail coverts. Apparently, then, the normal self-coloured bird has been subjected *to some factor which left the rectrices unaffected. When this factor* was removed (in the bright variety) the feathers of the rump were left in continuous series with the rectrices, no longer contrasting with them. On this hypothesis the grey rectrices of the dull bird would be due to an increase of the area subjected to the dulling

factor[1]. This and other similar suggestions will be discussed more fully at the end of the paper.

(*b*) *Scapular feathers.*

The anterior scapular feathers resemble those of the mantle in reproducing the patterns of the flank feathers of the normal bird, but among them I have not seen any on which the proximal bar has reappeared giving a false appearance of doubling. Among the posterior scapulars there is another and quite distinct type of doubling (Pl. XXIX, fig. 15) not seen on normal flank feathers. In this process the proximal bar has split, or been invaded by the chestnut of the fringe, so that the two resulting bars are separated, not by a pale bar, but by chestnut. Beyond the distal bar is a white fringe. In Fig. 15 a still further splitting is indicated.

The homologies of the bars may be tentatively summed up in tabular form:

rufa	*saxatilis*	*rufa* var. C	*rufa* C	*saxatilis*
flank	flank	mantle	posterior scaps	posterior sc
			(inner web)	(inner we
Grey base	Grey base	Pale grey	Yellow	Grey
Chestnut	Grey	Pale yellow	Chestnut-yellow	Chestnut-yel
Grey	Grey	Grey	Grey	Grey
Absent	Black	Black	*Absent*	Black
Pale	White	Yellow	Pale	Chestnut-yel
Black	Black	Black	Black	Black
Chestnut	Chestnut	Chestnut	Chestnut	Chestnut
—	—	—	Black	Black
—	—	—	Pale	Pale
—	—	—	Black	Black
Pl. XXVI, B	Pl. XXIX, fig. 10	Pl. XXIX, fig. 12	Pl. XXIX, fig. 15	Pl. XXIX, fig.

The grey and chestnut areas at the base have been included in the table but their homologies are not clearly understood; possibly they are in some way connected with the barring, *e.g.* the chestnut may have formed a complete ring with the apical chestnut, the whole pattern being a modified eye-spot. Of this nothing definite can be said.

(*c*) *Wing coverts and remiges.*

These are all patterned feathers, but to describe intelligibly the somewhat complicated arrangement of these patterns would be

[1] Obviously this representation might be inverted, the dull var. being regarded as due to loss, and the bright var. to addition. Between these two hypotheses we cannot decide. Whichever be adopted, the normal is the middle term.

difficult, and their bearing upon the more general problems has not yet been elucidated. Suffice it to say that a continuous series exists, passing down the inner covert feathers and then outwards through the secondary to the primary flights.

JUVENILE SPECIMEN (4) of *A. rufa*, bright variety (Lord Deerhurst's bird)

This bird, which is very small[1], *though superficially resembling the* other bright birds, differs from them in possessing a number of feathers of the first plumage, especially on the head and wings.

On the head, *black feathers have not yet appeared*—the small chick's feathers still persisting. Equally, the patterned feathers of the neck *are absent, the throat being entirely clothed in greyish juvenile* feathers. The breast has a mixture of grey feathers of the second plumage and pale chestnut feathers of the first. The feathers of the second plumage still retain their sheaths at their bases.

The flanks have the chestnut tips poorly developed, as is usual in young birds. *One of these flank feathers shows very slight indications* of a black bar outside the chestnut, followed by a further white fringe which is interesting since the true doubling of the distal black bar of the flanks is one of the unusual features of the corresponding variety of *A. saxatilis*, but is not found in the adult bright *A. rufa*.

In other respects the ventral side of the young bird is normal.

Dorsally, at a first glance, this bird is very different from the other bright birds. This is largely due, as were the abnormalities of the ventral side, to the presence of feathers of both first and second plumages.

Of the median dorsal feathers, those which are still in their sheaths agree closely with the feathers of the other bright birds. Those which are fully developed and about to be shed are almost devoid of barring, being pale chestnut with darker chestnut tips.

The scapulars and wing coverts include the same mixture of new and old feathers. The old feathers are of great interest since they agree more closely with the patterns of second plumage feathers of bright *A. saxatilis*. For example, many of these feathers have a heavy black bar on the outside while on the inside there are two bars

[1] For example the tarso-metatarsal is 32 mm. and the middle toe (without nail) *28 mm. against 41 mm. and 38 mm. in adult. An excellent account of the various* plumages of *A. rufa* at different ages is given by L. Bureau, "L'Age des Perdrix," *Bull. Soc. Sci. Nat. Ouest de la France*, 3e Sér. I, 1913.

separated by chestnut. The remainder of the feather is pale brownish yellow. Comparison with Figs. 8 and 9 in Pl. XXIX shows that these scapulars differ from those of bright *A. saxatilis* only in the loss of the proximal black bar, a difference which we should expect from the character of the normal flank feathers of the two parent species.

Between the anterior scapulars of the juvenile and adult bright *A. rufa* there is a much greater difference, namely, the true doubling of the distal black bar which has taken place in the first plumage only.

In the wing coverts there are similar points. Especially striking are the coverts which are next to the flight feathers. In the other bright *A. rufa* these have a black outer side and less developed black on the inside. The inside of each feather is covered by the outer web of its neighbour, so that in Plate XXVI these feathers show as a series of black lines. In the first plumage these feathers are black on the *inside* and pale on the *outside*, so that no black is visible externally when the feathers are in place. In the bright variety of *A. saxatilis* the corresponding feathers are black inside with some irregular black outside. In this point, as in the doubled bar on the flank feather and on the scapulars, the first plumage of bright *A. rufa* resembles the later plumage of the bright *variety* of the other species, *saxatilis.*

Alectoris græca saxatilis. "Bright" variety (var. *melanocephala* Fatio)

The general features of this form were described by Fatio, who applied to it the name var. *melanocephala.* In his paper there is a plate of this bird in black and white and coloured diagrams of several feathers.

In the light of what we know of the varieties of *A. rufa* it was very important to examine afresh the material which Fatio had described and to find out whether similar specimens of *melanocephala* had turned up since his description was published. As far as I know this has not occurred, but at Geneva there is a bird which will be described later since it shows some of the characters of var. *melanocephala* in a slight degree.

By the courtesy of the curators I was allowed to handle the specimens and to take several feathers from the Bex bird, of which some are figured in Pl. XXIX.

In this examination of abnormal *A. saxatilis* I set out to discover whether the variety was truly comparable with our bright *A. rufa,* *i.e.* whether precisely the same changes had taken place in the formation of the two varieties. Also I watched the seriation of the

patterns of the feathers in order to arrive at some general idea as to the sort of changes likely to be found in series of feathers, the patterns of which are meristic. In this paper I shall describe such details of the seriation of patterns as bear upon the first problem of the relations between the two varieties, mentioning in passing a curious case of pattern-reversal. At present it is not worth while to enumerate the many uncorrelated facts of feather decoration.

To explain the differences between the varieties it is necessary to bear in mind the differences between the parent species:

(1) The general body colour of *A. rufa* is reddish brown while that of *A. saxatilis* is grey.

(2) The striped flank feathers of *A. rufa* have only a single bar while those of *A. saxatilis* have two such bars (Pl. XXIX, figs. 5 and 10). As has already been mentioned this difference consists in the dropping out—in *rufa*—of the proximal bar which nevertheless occasionally reappears on the extreme anterior flank feathers (Pl. XXIX, figs. 13 and 14).

(3) The head and neck are very different in the two species. In each the throat is white and posterior to the throat is a black band, which curves down from the ears and is continuous mid-ventrally. Behind this in *A. rufa* there are many patterned feathers; these are absent from *A. saxatilis*, where the collar band is a very typical simple case illustrating the difference between *banding* and *barring*. At the anterior edge of the band in the median ventral line, the feathers are white at the base with a little black fringe at their tips. Behind these are feathers with rather more black. So, gradually, the black widens from a narrow fringe until it covers the whole feather, the white disappearing basipetally. This arrangement is modified in the var. *melanocephala*.

Description of *A. saxatilis* var. *melanocephala* Fatio

The general coloration of both specimens of this variety is very like that of the bright varieties of *A. rufa*. The head is black, the gorget is reduced, the back and wings are striped. But in the details there are several anomalous points.

The throat is white (*i.e.* normal) but the gorget shows the following seriations in the mid-ventral line: the first feathers have a greyish black fringe; in the following feathers there is a dark grey fringe and a dark grey base, leaving between the fringe and the base a paler bar. In feathers behind these, the fringe first fades away *in place*, then the

dark base disappears basipetally. In this region, where there was no barring in the normal, a form of barring has been developed resembling slightly that seen on the corresponding feathers of bright *A. rufa*, but differing markedly from the barring on the neck of normal *A. rufa*.

The flank feathers are very abnormal in the var. *melanocephala* (Pl. XXIX, fig. 7). The chestnut tip is much reduced—a juvenile characteristic present on the two specimens, one of which is adult. The two black bars have become very irregular and smudgy and in some cases fuse together in the centre of the feather. Many of these feathers show a true doubling of the distal bar. In Pl. XXIX, fig. 7, this is very poorly shown, but careful scrutiny reveals a paler, narrower triangle invading this distal bar from the left-hand side. This triangle is much clearer on the actual feather, especially when seen against a black background.

In the feathers of the lower breast and abdomen is another important difference between the bright variety of *A. saxatilis* and that of *A. rufa* where they remained normal. These belly feathers are in continuous series with the striped flank feathers. The barring has descended on to them so that they all show black lines on an otherwise self-coloured ground. On the more anterior belly feathers there are two such lines corresponding to the two lines on the flanks, but the feathers are somewhat asymmetrical, the distal band being most strongly developed on the outer side. This asymmetry is what we should expect from the character of the normal flank where the more ventral feathers have the bars less formed on the ventral (or inner) side.

Posterior feathers of the belly have no distal bar which faded away in place, but the proximal bar remains on the yellow chestnut ground. The symmetry has undergone an unexpected change, the bar being best developed on the median side of the feathers. Traces of the black bar are on all ventral feathers, even the small feathers immediately in front of the anus having blackish smudges.

Dorsally this variety agrees with the bright form of *A. rufa*, as has been stated, and still more exactly with the first plumage of that variety. Among the median dorsal group of feathers those of the mantle have the proximal bar characteristic of the species poorly developed. The distal bar has partially undergone true doubling; so that on each side there is a horseshoe-shaped black mark filled up by chestnut which has come in from the outer side. On the more lateral

feathers of the group—*e.g.* feathers from the same region as Figs. 3 and 12, Pl. XXIX, which are from *A. rufa*—the distal bar is single on the outside and very broad, while on the inside web the true doubling persists. Feathers of this type are common on the back of this variety, as they are on that of the juvenile bright *A. rufa* in its first plumage.

Posteriorly in the median dorsal group the old proximal bar disappears in place, the distal bar persists very broad on both sides of the feather and frequently shows its double nature by partially dividing, leaving chestnut between the two bars so formed, as it did in the first and later plumages of the bright *A. rufa*. This bar gradually fades away in place, giving a complete seriation of colours down the back to the still normal rectrices.

The scapular feathers (Pl. XXIX, figs. 8 and 9) have the proximal bar well developed, but asymmetrical. Fig. 8 shows a feather of a common type from the left side of the bird. On the outside web is a single black bar of doubtful homology, probably a fusion of proximal and distal bars, judging from other similar feathers on which this external bar is better developed. The grey reaches clearly up to it and there is a slight invasion of the bar from the rachis by a paler triangular area. On the inside web there are three bars, viz. a true proximal bar and a doubled distal bar.

Among these patterns there occurs a reversal of symmetry quite unexpectedly. Pl. XXIX, fig. 9, represents one of these reversed patterns. The feather from which the figure is taken lay immediately under that shown on Fig. 8. It will be seen that the outside web of Fig. 9 is a very fair mirror image of the inside of Fig. 8. But on the inside of Fig. 9 the copying is not so exact and, instead of the single bar, which was described above as a fusion of the proximal and distal bars, we get two bars, the proximal having shifted outwards towards the distal bar without fusing with it.

This reversal seems to us very remarkable. It is present on both sides of each of the two specimens of the var. *melanocephala* but it only affects a very small number of feathers in each case—three at most. There are occasional feathers of intermediate symmetry, of which we have one on which there is a proximal bar on the same part of the web on each side, while the distal bar is symmetrically doubled. The feathers on *A. rufa* corresponding to these reversed feathers show but little change of the same kind; the chevron mark is perhaps somewhat altered, but initially it was so nearly symmetrical that no

conclusions can be drawn from this. No hypothesis can at present be put forward to explain the reversal beyond saying that the scapular pterylosis perhaps constitutes an *independent* system of symmetry—independent of the more general controlling mechanism which lies behind the bilateral symmetry of the body as a whole. This emancipation of the scapular pterylosis is perhaps correlated with the increase of barring, since it is possible that the latter is an effect of some change whereby the feathers have been allowed to act as individuals with their own pattern-control, independent of the more general system which lies behind the *banding*.

The wing coverts need not be described at length apart from mentioning again the symmetry of the coverts which overlie the flight feathers—one of the points of agreement between this variety and the first plumage of the bright *A. rufa*. The seriation of patterns follows much the same lines as in *A. rufa*.

The secondary remiges are pale feathers with black tips and irregular blotches of black on the centre along the rachis. This black increases from feather to feather as we go outwards until on the outer primaries there is only a very little pale colour in broken patches on the inside of the feather. The primaries have no chestnut on the basal region of the outer vane to correspond with the chestnut present on the adult bright *A. rufa*. This chestnut is absent too from the first plumage.

THE GENEVA SPECIMEN. (Partially "bright" *A. saxatilis*, No. 3)

When on my way to Bex and Sion to see Fatio's birds, I stopped at Geneva and visited the University Museum to look for any variation which might bear upon the two aberrations. I found there one very interesting specimen of *A. saxatilis*, a female, which had a few abnormal striped feathers on the back, and in a small degree some of the other characters of Fatio's birds. I made a description of this bird before I had seen the two bright specimens at Bex and Sion, so that the description here reproduced was not affected by a knowledge of the details of those birds.

Description. The general colouring and size are normal. The head and throat are normal, but the black gorget is somewhat reduced ventrally. This is quite marked: there are fewer black feathers and less black on them. The breast is normal. The pale brown belly is normal.

The barring of the flanks extends *further ventrally than usual*. This may have been due to the method of stuffing, but I considered this possibility at the time and made a note saying that I did not believe

that the abnormal appearance was due to this. The skin has been sewn up in such a way that the mid-ventral seam is pushed inwards, a distortion which might cause the flank feathers to appear to extend towards the mid-ventral line. The symmetry of the flank feathers is normal. The rectrices are normal.

On the back there are seven abnormal feathers which I described as being all in the scapular pterylosis, though when I took my notes I was not fully able to separate mantle feathers from those of the scapular region. It appears from the curvature of the specimen in Pl. XXIX, fig. 11, that the feather belongs to the mantle.

On the right side there were three barred feathers inserted close together in what I then regarded as the posterior part of the scapular pterylosis. They all had the same type of pattern and asymmetry which were best developed on the posterior of the three feathers and least clear on the middle feather. (The posterior feather is reproduced in Pl. XXIX, fig. 11, thanks to the courtesy of M. Bedot, the Curator of the Museum.) The aftershafts of these three feathers were paler than those of their neighbours.

On the left side there were four abnormal feathers, three of which were inserted close together, forming a small patch somewhat posterior to the corresponding patch on the other side of the back. The patterns and symmetry were substantially similar, the feathers on the left being mirror images of those on the right. The bars were much more indefinitely formed. The fourth feather on the left side was much further forward, having its tip near the angle of the wing.

There were no other abnormalities in the colour of this bird, except a few irregular spots of black on one or two of the mantle feathers.

Thus the bird has the following points in common with the var. *melanocephala*:

(1) Seven barred dorsal feathers.

(2) Some ventral extension of the barring usually confined to the flank feathers.

(3) Some reduction of the collar band.

G. B.

Discussion

Nature of the Aberrations

On this head we have little to remark. Nothing suggests that either aberration is a product of hybridisation and that hypothesis may be dismissed. Those who are interested in the evidence as to alleged

hybrids of *Alectoris* or of *Perdix* will find a full collection of records and discussion in Suchetet's most valuable treatise[1]. Amongst various suspicious cases Fatio's specimens are considered by Suchetet and we are satisfied that readers will agree with him that the "bright" variety of *A. saxatilis* cannot have resulted from hybridisation with any other species[2], though with doubt Suchetet admits that certain other specimens may have been true hybrids between *rufa* and *saxatilis*. Our two aberrations of *A. rufa* were not known to him. To Suchetet's discussion we may add that not only is a cross with some other species of Partridge ruled out, but, apart from several other considerations, the absence of the slightest structural departure from the normal disposes of any idea—in any case very remote—that crosses with domestic poultry can have produced these results.

No opportunity has yet occurred of making a histological examination of the genitalia of these aberrations. Though such examination is desirable we see no reason to anticipate that any form of pathological sterility is responsible for either. In both *rufa* and *saxatilis* the sexes normally differ very little, if at all, in plumage. Externally, apart from the presence or absence of spurs they cannot be certainly distinguished from each other and it is therefore almost out of the question that either aberration, still less both, can be a consequence of sexual derangement. It is to be remembered that the three dull *rufa* were males, and at least two of the bright *rufa* are also males. The third bright *rufa*, though the sex is not recorded, is almost certainly ♀, since though a full grown bird no spurs are developed. One of the bright *saxatilis* is ♀, and the Geneva *saxatilis* which had some "bright" features was also ♀. As regards the bright aberration therefore we have proof that it may manifest itself in either sex[3].

We look on the two aberrations as due to changes in the factorial composition of the normal, proceeding in opposite directions, but as to the physiological cause of these changes we have no suggestion to offer.

[1] A. Suchetet, *Des Hybrides à l'état sauvage*, Lille, I, 1896, *Classes des Oiseaux*, pp. 6–10 and 485–499.

[2] Incidentally he mentions, pp. 9 and 487, a bird in the Museum at Marseilles as possibly a further specimen of Fatio's var. *melanocephala*.

[3] It is perhaps worth noting that probably none of these females were sexed by their genitalia and that we can only guess at the effects of pathological sterility upon the spurs, but since the Norton Hall bright bird has very large spurs, and the Kinver bird though adult has none, sexual disturbance cannot be suspected as the source of the aberration.

The Nature of the Factorial Changes

No attempt to bring the several forms into one consistent scheme of factorial representation has been successful. In our present ignorance of the mechanical and chemical processes by which pigments are distributed over the surface of the body such hopes can be scarcely entertained. Nevertheless, on comparing the dull, the normal and the bright birds together, their distinctions may evidently in part be represented as a series of terms in the development of colour-segmentation. In the dull bird no segmentation or barring of colour occurs, whether on single feathers or as affecting groups of feathers except on the neck. In the normal, barring has occurred on the feathers of the flank, and in the bright birds this process is extended over the mantle and scapulars and in bright *saxatilis* over the belly also.

For such a series of terms in the progressive spread of barring analogies may be found in the banding of the Equidæ. In the various species of Asses stripes may be absent or only slightly developed on the extremities. In the extinct Quagga (*Equus quagga*) the striping was complete on the head and was continued backwards over the withers and thorax, dying out in the middle of the body, leaving the hind quarters and legs self-colour. In the Zebras this striping is complete over the whole body and legs, the light-coloured belly alone excepted. But the other changes in the partridges appear to he independent of the spread of barring.

Nevertheless the various distributions of the colours in the rectrices and tail coverts obviously form a progressive series of three successive terms of which the normal is again the middle. In the dull birds the whole tail with its coverts is approximately of one colour. In the normal the rectrices are chestnut with the coverts unaffected. In the bright birds the chestnut of the rectrices has spread up to include the tail coverts.

If these were the only distinctions the three terms would naturally be regarded as ordinary progressive distinctions, which, if referable to genetic factors, would on analysis presumably fall into a multiple allelomorphic series; and though making no suggestion as to which end of the series should be regarded as positive and which negative, we incline to accept this interpretation. When, however, we come to the characters of the head and throat we are at a loss. The three arrangements appear to be entirely independent of each other, nor

can we suggest any way in which any one can be readily interpreted as a derivative of any other. The greatest difficulty arises in connection with the black head of the bright variety, which is probably a definite accompaniment of that variety in both the species concerned, for, as stated above, we incline to interpret the head of Lord Deerhurst's bird as differing in juvenility only. We have to remember that a form exists in south-west Arabia which has a black head, the species *melanocephala* Rüpp. This is evidently a distinct species, characterised by great size and certain peculiarities of coloration, amongst which a black head is the most striking feature. This black head may no doubt be factorially of the same nature as that in the bright varieties of *rufa* and *saxatilis*, but nothing else in the plumage of this species *melanocephala* is suggestive of the other distinguishing characteristics of our bright birds.

If the features of the throat stood alone we might perhaps incline to conjecture that the dingy throat and weakly marked gorget of the bright birds meant that the normally sharp differentiation into white and black was suppressed, just as the waves of differentiation die out on the Quagga. On another line of interpretation the black throat of the dull birds might be supposed to be the black of the normal gorget which had not been pushed back into its typical position. But there is little to commend such suggestions, and we see no scheme by which analysis of the distinguishing features of the head, throat and breast can be attempted.

Very similar and equally insoluble difficulties arise in regard to the features distinguishing the head and neck in the varieties of *Colaptes* (the American Flickers, Picidæ) known as *auratus*, *cafer* and *chrysoides*[1]. Here again we have varieties in which certain distinguishing features cannot be represented as in any sense readily transformable into each other. For example, in *auratus* the throat and foreneck are brown, and the top of the head and the hindneck are grey, but in *cafer* the colours are exactly reversed, the dorsal parts of head and neck being brown and the ventral part grey. Moreover the development of the other distinguishing marks, especially the nuchal crescent and the colour of the malar stripes, cannot be readily ascribed to the operation of a single factorial element. Nor have we any indication to guide us in the attempt to decide which of the varieties is due to a factorial gain and which to a factorial loss.

[1] For an account of these see W. Bateson, *Problems of Genetics*, New Haven, 1913, pp. 147–156, coloured plate.

Besides the species, *A. melanocephala*, mentioned above, there is another related species which may throw some light on the increase of barring, namely, *A. petrosa*, in which the scapulars are normally somewhat patterned. The feathers have bluish-grey centres and bright chestnut margins. The chestnut is sharply separated from the grey but there are no black bars. Extreme anterior flank feathers of normal *A. rufa* have somewhat this appearance, so that perhaps in *A. petrosa* the barring has normally an influence on the scapular feathers.

In attempting to form a conception of the way in which rhythmical banding develops and spreads over the body of an organism, or rhythmical barring over an organ such as a feather, the analogy with the propagation of wave-motion must in part, at least, be a true guide[1]. The terminology is immediately applicable. As Whiting, for example, has done in a discussion of the banding of Cats' skins, we may in such cases perhaps speak of these bands as "waves of pigment-forming metabolic activity[2]," and the terms "crest" and "trough" which he has used in reference to the banding of a moth's wing[3] are probably more than merely metaphorical expressions. We may even go further, and applying the analogy of wave-length we may speak of the pattern on Grévy's Zebra (*Equus grévyi*) as approximately the upper octave of that of *Equus zebra*. Such a terminology by familiarising the mind with the probable nature of the process of these segmentations will prepare the way for a correct analysis, though admittedly open to abuse.

Attention is finally called to the curious development of a minor system of symmetry in each scapular region in the bright varieties, as indicated by the occurrence of feathers within one pterylosis which are partially mirror-images of each other.

In the course of our inquiries we have had help from many ornithologists. We feel under a special obligation to Mr P. R. Lowe for entrusting us with this curious and valuable material. Our thanks are due both to him and to Mr N. B. Kinnear of the British Museum for their continued help in a field with which we have little familiarity.

For assistance in connection with the study of the specimens in Swiss Museums we must express our gratitude to M. Paquier of Bex, who gave special facilities, to M. C. Meckert of Sion and to MM. Bedot and Revillod of the Geneva Museum.

[1] See especially *Problems of Genetics*, 1912, Chap. III.
[2] P. W. Whiting, *Journ. Exp. Zool.* XXV, 1918, p. 551.
[3] *Ibid.* XXVIII, 1919, p. 440.

NOTE. After this paper had been written we learnt through the kindness of Mr Lowe of two more specimens of the "bright" variety of *A. rufa* killed in Spain. He sent us a paper[1] by Ignasi de Sagarra in which the second of these, found near Valencia, was described with figures and a good coloured plate. The bird agreed in all respects with our var. *melanocephala*, and it apparently resembled the Overbury bird in having a nuchal band. Sagarra refers to two papers by Soler[2] dealing with the earliest specimen, the locality for which is given as "Sant Llorenç del Munt" in the extreme east of Spain.

Both birds had some greyish feathers scattered through the black cap which Sagarra regards as transitory and possible indications of changing plumage.

Both authors consider these birds as belonging to a new species. In his first paper[2] Soler called it *Perdix melanocephala*, but in a further note in the same Journal[3] he substituted the name *Perdix ornata*, since *melanocephala* was already in use for the Arabian species.

We cannot find the particular San Lorenzo, but Sagarra's remarks indicate that (p. 9) it must be more than 200 miles from the Valencia locality.

Soler's bird was found among normals. Sportsmen in the previous year had, however, mentioned seeing similar birds which they had called "*Perdius canaris.*"

Finally, as the sheets were passing through the press, we have found a letter by A. Vaucher (*Boll. Soc. Ticinese Sci. Nat.* VIII, 1913, p. 106) addressed to Ghidini giving various details as to the variability of *saxatilis*. For the most part these appear to have no direct relation to our problems, but M. Ghidini appends this interesting note: "J'ai observé souvent sur le croupion des bartavelles, des plumes qui montraient une coloration se rapprochant de celles des flancs, presque toujours par groupe de trois: p. ex.: une femelle du Val Bavona du 31. I. 1911." Evidently the reference is to such specimens as the Geneva bird from Orsières, which had been presented by M. Ghidini himself. These *saxatilis* with chevron feathers on some part of the back "*par groupe de trois*" may be regarded as another term in the series between the normal and the var. *melanocephala*.

[1] L. de Sagarra, "Noves Ornithòlogiques," *Treballs de l'Inst. Catalana d'Hist. Nat.* 1915, p. 5.

[2] *Butlletí Inst. Cat. d'Hist. Nat.* 1904, p. 51, with a photograph.

[3] *Ibid.* 1906, p. 16.

DESCRIPTION OF PLATES

PLATES XXVI AND XXVII

Alectoris rufa. In each plate, A is var. *obliterata*, the Braintree specimen of the "dull" variety. B is the normal. C is the var. *melanocephala*, the Norton Hall specimen of the "bright" variety.

PLATE XXVIII

Individual feathers taken from positions, approximately corresponding, on the left side in the three forms. A, B, C, the three forms as before, but the feathers are not in each case all from one specimen.

Fig. 1. Flank. Fig. 2. Breast. Fig. 3. Median wing covert.
Fig. 4. Anterior part of mantle. Fig. 5. Back.
Fig. 6. Rump. Fig. 7. Belly. Fig. 8. Lower neck.

PLATE XXIX

Figs. 1–6 *Alectoris rufa.*

Figs. 1–3 are left mantle.

Fig. 1. Dull variety. Fig. 2. Normal. Fig. 3. Bright variety.

Figs. 4–6 are from the right flank.

Fig. 4. Dull variety. Fig. 5. Normal. Fig. 6. Bright variety.

Figs. 7–11 *Alectoris saxatilis.*

Fig. 7. Var. *melanocephala* Fatio, the Bex bird. Right median flank feather, showing some chestnut invading the black bar.

Fig. 8. Var. *melanocephala* Fatio, the Bex bird. Left posterior scapular of the usual pattern, with ashy blue area on the external web, and three dark bars on internal web.

Fig. 9. Var. *melanocephala* Fatio, the Bex bird. The exceptional or "reversed" pattern with trace of ashy blue area on internal web (scarcely visible in the colour print) and three dark bars on the external web.

Fig. 10. Normal flank feather (left median).

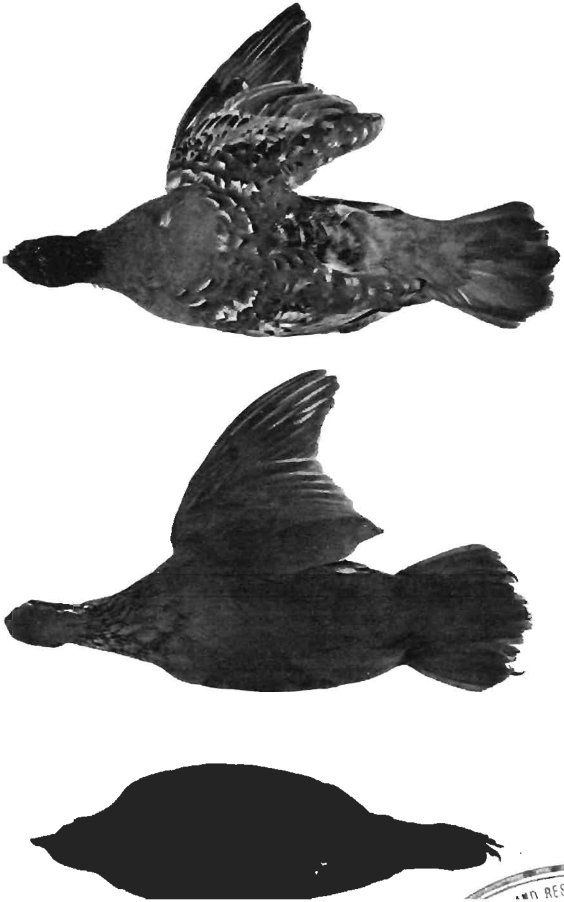
Fig. 11. Right scapular (or mantle?) from the Geneva specimen of *A. saxatilis* showing the pattern peculiar to var. *melanocephala* Fatio. One of three such feathers in this position.

Fig. 12. A left mantle feather of *A. rufa*, var. *melanocephala*. British Museum mounted specimen Reg. No. 1904.10.2.1, showing the proximal bar exceptionally well developed. Compare Fig. 3 on same plate which shows the usual appearance of such feathers in this variety.

Fig. 13. *A. rufa*, normal. Right anterior flank feather showing the proximal black bar on external web.

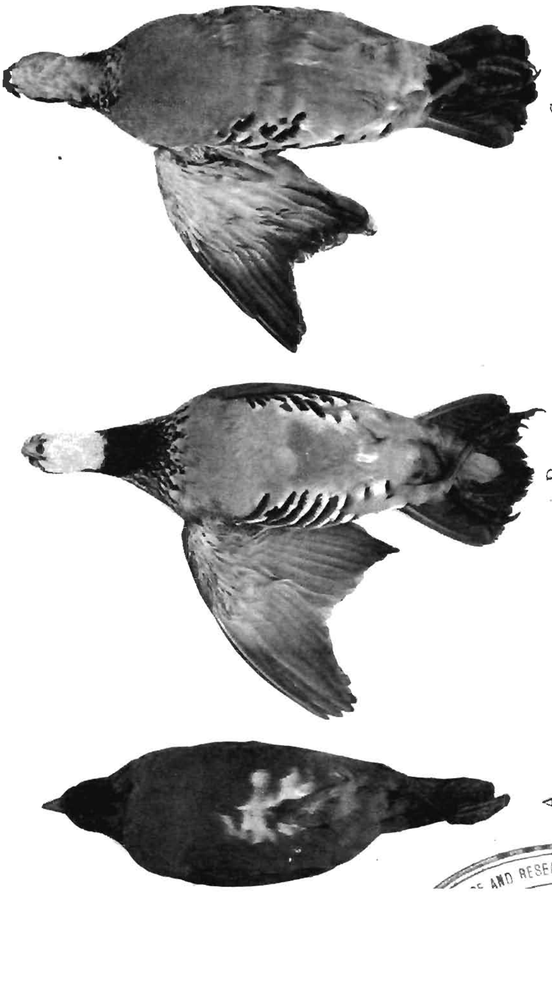
Fig. 14. *A. rufa*, normal *juv.* Right anterior flank. Proximal black bar on both webs, as in normal *saxatilis*. Such feathers are uncommon in *A. rufa*, and occur only at the anterior end of the scapular series.

Fig. 15. *A. rufa*, var. *melanocephala*: left posterior scapular, showing doubling of the distal black bar.



AND RESEA

PLATE XXVI



A B C

...AND RESEARCH

PLATE XXVIII

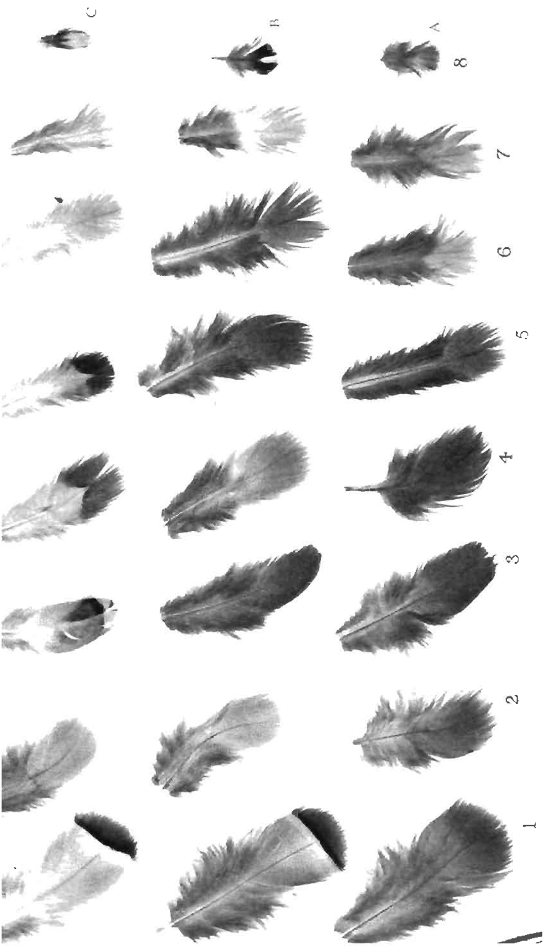
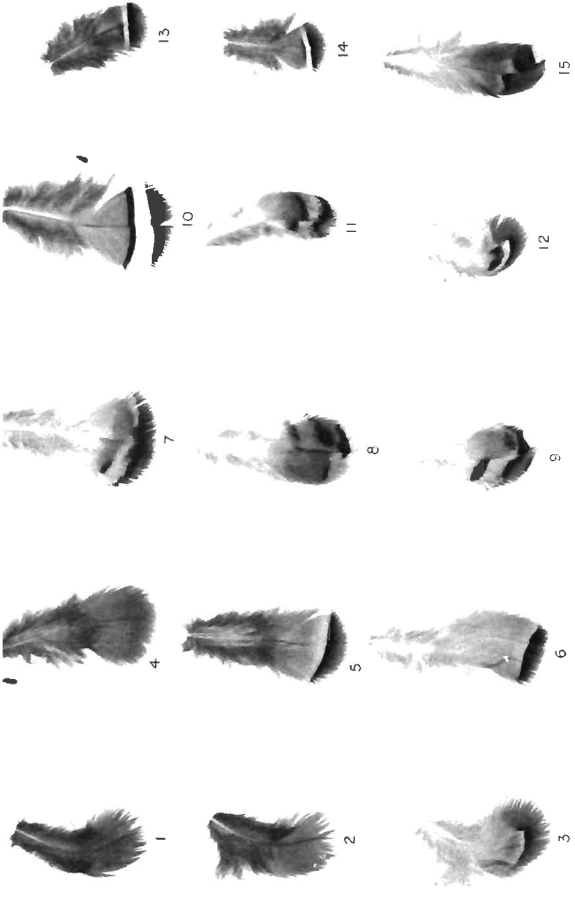


PLATE XXIX



SEGREGATION

[*Journal of Genetics*, xvi, 1926]

Introduction

In 1922 I had the honour of delivering the Leidy Memorial Lecture at Philadelphia. The substance of that address is embodied in the following paper. I was reluctant to publish it immediately for several reasons. The evidence to which I appealed had not all been fully tested. Some also might be disposed to set aside the phenomena adduced, on the ground that they are exceptional and of small immediate significance pending the determination of the broader principles.

Experience has meanwhile provided confirmation where it was required, and several of the classes of segregation which might formerly be held peculiar or anomalous, have been demonstrated in such abundance that no survey of genetical physiology can disregard them. In so far, moreover, as I was concerned with principle, I wished for opportunities of hearing the criticism of other geneticists holding different opinions; but after many such debates I have learned nothing which appears to dispose of the views to which I inclined.

The growth of genetical science has been surprisingly rapid. To those who have not forgotten the period of stagnation which so long continued, such an activity can only be a source of satisfaction, as implying zeal both in observation and invention. We do well, however, to remember that that long spell of dulness from which we were so lately emancipated, ensued as the direct consequence of a too facile acquiescence in impermanent doctrines. Curiosity was too easily allayed. We are in no such danger yet, but the following pages may at least serve as a reminder that, even as regards the outline of genetical principles, finality has not been attained.

1. The Nature of Segregation

Segregation is the central phenomenon round which the modern conceptions of genetics have been developed. Two questions regarding segregation may be asked with some hope that observation may provide an answer. First, what in the act of segregation separates from what? Secondly, when, at what moment or moments in the life-history of an animal or plant, does this separation occur?

In the first of these questions we are obviously considering a matter of fundamental importance. Let us begin with segregation in respect of any factor in the homozygous state. Whichever the critical division may be, it normally then results in the formation of two similar products. All that we know is consistent with the belief that segregation in this case is the segregation of two *similar* things, upon whatever their ultimate properties depend. Here the conception of allelomorphism raises no difficulty. Whatever is taken by the one half resulting from the critical division, is identical with that which is taken by the other half. But when segregation is effected between the dividing cells of the heterozygote, the consequence of that process is that the two halves differ in some demonstrable respect, being unlike in their genetical powers. Though wholly ignorant even of the proximate elements upon which these powers depend, we are nevertheless tempted to form some conception of the nature of the unlikeness between the resulting halves.

We distinguish at once two possibilities. The distinction between the two halves may be due to the presence of something in the one which is absent from the other, or it may be attributed to the presence of a different positive and effective determinant in each of the two halves. The first of these interpretations is known briefly as the Presence-and-Absence hypothesis. From an early stage in the development of Mendelian analysis that supposition has seemed to me a reasonable one, furnishing, as it does, a concrete and acceptable account of the nature of allelomorphism—a relationship otherwise mysterious and paradoxical—with the additional merit that the basis for a simple and widely applicable notation is immediately provided. This representation has the advantage of extreme simplicity. It implies only that something, whether a material something or otherwise, is present in the one half which is absent from the other, and it is equally applicable whatever the future may reveal as to the ultimate nature of the factors, and whether the distinction prove to be one of material, or, for example, to take another possibility, of potential.

With the supervention of the chromosome theories, for reasons which I have never clearly understood, the interpretation based on Presence-and-Absence was set aside. Objection can scarcely be taken on the ground that no cytological distinction is normally visible between the two halves. Though intelligible as a reminiscence of the period in which whole chromosomes were looked upon as possibly responsible for separate factors, that consideration has little weight

now that every chromosome is regarded as the possible bearer of countless genes. The expectation that the absence of even a large number of genes might make a difference distinguishable to the eye, with the means at our disposal, is one that even the crudest form of the hypothesis of transmission by chromatin would scarcely lead anyone to entertain. Moreover, whatever cogency such argument might have possessed so long as the male Drosophila was believed to have no Y chromosome, disappeared when a Y was found and, though present, was found to be devoid of genes.

The contrast between the two modes of representation reaches a climax in the expressions which we should respectively use to denote the genetical constitution of two white-flowered races which, as in Sweet Peas, may when crossed give a coloured F_1, followed by 9 coloured : 7 white in F_2. For Morgan the two whites, though alike and indeed indistinguishable without the breeding test, "are the product of different factors[1]." To complete the statement I suppose we might next declare that the white in F_2 which gives *no* colour when crossed with either parent race is the product of the two different factors for white combined. The same reasoning would be applied to all examples in which two similar recessives when crossed reproduce the normal dominant. Surely the invocation of these positive elements to "produce" the recessive character is here evidently superfluous. The whites are all alike whites. Some are reduced by whiteness through the loss of one of the complementary elements—in our notation C, some inasmuch as they are destitute of the other, R, others again inasmuch as they have lost both. Nor is the distinction one of words merely, for according as one or the other representation is adopted our conceptions of genetical physiology will be greatly changed.

The argument most frequently specified as militating against Presence-and-Absence is derived from the phenomenon of multiple allelomorphism. When Johannsen[2], for example, adopts the American view, speaking of the Presence-and-Absence hypothesis as "now abandoned," it is upon the multiple series that he apparently bases his judgment. Rightly regarded, however, I contend that the multiple series not merely contribute nothing capable of such construction, but that their existence amounts almost to a demonstration of the correctness of the Presence-and-Absence hypothesis.

In developing his criticism of that hypothesis, Morgan remarks that

[1] *Mechanism of Mendelian Heredity*, ed. 2 [1923], p. 36.
[2] *Hereditas*, IV, 1923, p. 138.

"it is a characteristic of 'multiple allelomorphs' that the same character is affected[1]." Apart from exceptions not yet well defined, this is true, and the fact is of great significance. The statement should be amplified, and may be put in the form that, apart from the exceptions, factors composing a multiple allelomorphic series produce an effect in degrees quantitatively different. The factors composing any such series may thus be arranged in a descending scale. This is exactly what is expected. The factor put in on the one side is absent, wholly or in part, from the other, and, on segregation, the two qualities which respectively were combined in fertilisation, reappear. Why Morgan should declare that "only one kind of absence is thinkable[2]," I do not understand. We should not assert that because a sovereign is absent from a purse, that purse must contain nothing. Surely my opponents must sometimes wonder why, according to the views they entertain, the relation of allelomorphism so constantly exists between positive and negative in a single respect; since, if they deny these relations to be a matter of quantity, allelomorphism might be expected to manifest itself just as often in a relationship between characteristics having no perceptible connection with each other.

When we find, as we do in a series of Multiple Allelomorphs, that the relationship holds, not only between one pair of quantitative differences, but between a whole graduated series of such differences, the nature of that relationship might be regarded as settled beyond dispute. We have been asked to conceive of each allelomorph in any pair as equally a positive something. In a multiple series, are we then to suppose that as the allelomorph *of each grade* in the series a corresponding positive something exists? Such an interpretation verges on absurdity, and the multiple series are a clear demonstration that allelomorphism is not a haphazard relationship between two independent features, and as good a proof as we can possibly expect, that that relationship involves and implies a distinction in some quantitative respect.

The quantitative distinction may of course manifest itself in various ways. The consequence of fractionation may appear, for example, as either a diminution of the area affected, or in a reduction of intensity of an effect, and doubtless in other ways also.

When the nature of these quantitative series is properly understood we obtain a simpler and clearer conception of the meaning of factors

[1] *Mechanism of Mendelian Heredity*, ed. 1915, p. 168; ed. 1923, p. 215.

[2] *Physical Basis of Heredity*, n.d., p. 251.

for pattern, for extension, for intensification or dilution, and the like, which now form so large a part of our analytical apparatus.

As the simplest possible illustration of how the quantitative hypothesis may be applied to the representation of a multiple series, take the yellow "eye" of *Primula sinensis*[1]. As a matter of history the middle term in the series is the original normal. The eye extends over about $\frac{1}{4}$ or less of the limb. In a recessive form, "Primrose Queen," it extends over about $\frac{1}{2}$ of the limb. The form with more white is completely dominant. Obviously we may say that there is something present in this organism which represses the development of the yellow in the middle third. Later appeared "Queen Alexandra," in which there is barely a trace of the yellow eye. Whichever of the first two is crossed with this top dominant, the result is the same, and the eye of F_1 is almost or quite as pale as the eye of "Queen Alexandra." The three terms behave as multiple allelomorphs:

W makes the whole petal white, as in Queen Alexandra.

$W - \frac{1}{4}$ (as an approximation) leaves the band of yellow in the normal.

$W - \frac{1}{2}$ allows the extension of the yellow over a further segment, as in Primrose Queen.

Possibly W may be still further diminished, but representation of the terms already known suffices for present purposes. Subsequent discovery of other terms in the series can in no way disturb the applicability of this system. So long as nothing lower than Primrose Queen is known, that may be taken as the basal negative.

Colour in the Rabbit may be taken as an illustration of somewhat greater complexity. Self-colour with dark eyes, the Himalayan and the albino, both pink-eyed, together form a multiple series. From whatever parentage the albino be derived, it cannot, crossed with the Himalayan, produce a dark-eyed or a self-coloured form. On the other hand, the allelomorphism of self, Dutch, both dark-eyed, and the albino does not involve a multiple series. Dutch crossed with albino gives either Dutch again, or an approximately self-coloured animal, according to the factorial composition of the albino. The nature of this distinction may be very simply expressed. We may describe the Dutch and the Himalayan as each wanting in some portion of the full complement needed to confer self-colour, but the ingredient missing from the Dutch is not the same as that missing

[1] See *Journ. Gen.* XIII, 1923, p. 226, and Pl. XVII, fig. 35. [This vol. p. 343 and Pl. XXIV, fig. 35.]

from the Himalayan. Nor are the factors for these two ingredients allelomorphic to each other. If we call C colour and S the element conferring self-distribution, then the Dutch has $C\frac{S}{2}$ and the albino either cS or $c\frac{S}{2}$,—the one capable of turning Dutch into Self, the other leaving it Dutch[1].

But the Himalayan is deficient in another ingredient. For simplicity we suppose this to be the C spoken of above. The C, $\frac{C}{2}$, c, form a multiple series; and the Himalayan bred to the Dutch has the power of making F_1 *Self*, since, though having only half of C, it has the whole of S. Thus:

Dutch × *Himalayan*

$$C\frac{S}{2} \qquad \frac{C}{2}S$$

$$F_1 \text{ Self } C\frac{C}{2}S\frac{S}{2}$$

F_2	*Self*	*Dutch*	*Himalayan*	*Dutch Himalayan*
	CS	$C\frac{S}{2}$	$\frac{C}{2}S$	$\frac{C}{2}\frac{S}{2}$

In F_2 there are of course animals, otherwise Himalayan, but deficient in some of the colour proper to a correct Himalayan. They are mentioned by Punnett[2] as "full Dutch Himalayan" and they have more or less white on those parts which, though coloured in correct Himalayans, are white in the Dutch. Evidently all albinos contain S in some degree, though the quantity may be small and result in the very low terms in the Dutch series like those which Castle has figured[3]. If albinos altogether devoid of S existed, we should have 9 coloured to 7 white in F_2, and, subsequently, extracted albinos capable of giving coloured offspring in their crosses, neither of which results has been

[1] The expression $\frac{S}{2}$ is not intended to mean that the factor S is exactly halved in the Dutch. As in some similar examples, the fractionation of this factor is very indefinite. Probably no strain, even of thoroughbred Dutch, shows uniformity in correct marking; and, as Castle has shown, there are very many grades which have overlapping fluctuations. The Primula eyes are indeed somewhat exceptional in the sharpness with which their quantitative grades are defined.

[2] *Journ. Gen.* II, 1912, pp. 237–8 and Pl. XIV, fig. 2.

[3] *Carnegie Inst. Publ.* 1919, No. 288, Pl. I.

seen in rabbits. The fact that an albino may contribute a factor which can raise the Dutch up to self-colour proves that after all the colour of the animal is like that of the plant, in that it is due to the interaction of complementary elements, although since one of them is never wholly absent, we do not meet with the production of colour from two albinos. Self and the various grades of Dutch are probably related as a multiple allelomorphic series, though, as explained above, the graded factor is not that which is responsible for the self-Himalayan-albino series. When the chemistry of colour-production is understood more fully, we may find that the element in the animal which I here speak of as S may be analogous with one of the two complementaries of the plant; and that the distinction between the self and the picotee in the Sweet Pea is due to quantitative differences in an element playing the same part as that which by its quantitative grades distinguishes the self from the Dutch in the rabbit.

When we come to the mouse, a further term appears. For the pink (really *pale*) eyed mouse, with dilute-coloured coat, crossed with certain albinos, may produce dark-eyed F_1 (whether self-coloured or piebald). The allelomorphism is not here multiple, and we are thus precluded from regarding the pale eye and the weakness of the coat colour as simply degradations of the rabbit's factor C. Nor are they due to one of the stages of S, for that is concerned with the area of the coat colour. For clearness we must use a fresh term, P, the factor which can turn the pink eye dark, and the coat deeply coloured, when it is in combination with C. So the pale-eyed with light coats are pC, and the albino is either pc or Pc.

We cannot as yet positively declare how these factors in the Mouse are related to those in the Rabbit. Sewall Wright[1] has done this with considerable success for most of the series in mammals, but I do not understand that the particular problem here in question is dealt with in his scheme.

When the factorial scheme is thus set out, we obtain a clear suggestion of the nature of a "pattern factor." The colour of the Dutch Rabbit has its peculiar distribution because some ingredient necessary to the formation of pigment is actually missing from the parts which remain white. One of the ingredients—say the enzyme—is not broken

[1] *Amer. Journ. of Hered.* VIII, pp. 224, 373, 473, etc. The graphic method of representation which he has suggested has great advantages, and comes nearer to giving a rational and acceptable picture of the phenomena than any I have seen elsewhere. (See especially *loc. cit.* p. 230.)

up piebald-wise, but extends over the whole skin and eyes. The other, presumably the chromogen, is wanting from the white areas. Rabbits do not, I believe, show ghost marks, but where those marks exist I can scarcely doubt that they indicate the actual presence of a material due to the activities of some factor, which comes thus to be regarded as responsible for a pattern. The question, which ingredients can be broken up and which cannot, has probably much biochemical significance. We may declare, for example, that the existence of tricolour guinea-pigs means that in that animal not only the chromogen but also the element which can turn red into black, may be broken up into piebald areas, whereas the non-existence of tricolour mice and rats means that in them this element (Sewall Wright's Enzyme II), or its product, always pervades the whole skin. Similar interpretations are probably applicable to all pattern factors, and bring tbem at once into accord with the quantitative system of representation.

The quantitative system commonly obviates the hypothesis of complete linkage, to which recourse is sometimes had by those reluctant to recognise the existence of multiple series.

This appeal to linkage, as it seems to me, leads to further embarrassments. If a multiple series really relates to "the same character," the quantitative system is a sufficient, and, as I think, a more probable representation of the phenomenon. I know as yet of no series proved to be multiple, in which the several terms in the factorial series have effects manifested in apparently unrelated physiological consequences. The series most nearly fulfilling this condition is that originally discovered by Nabours in *Paratettix*. The distinctions there, as Morgan says, are all matters of "colour"; but when colours not merely take the form of reds, yellows, etc., which can reasonably be interpreted as modifications of a single pigment, but include also the development of a dense white, obviously consisting of a wholly distinct material, that coloration is not readily to be accepted as a single character. That in Nabours's segregation linked factors, or groups of factors, are concerned (in addition to multiple series), seems highly probable; and indeed, in the later phases of his work, some distinct evidence of crossing-over was obtained. Pending an extended study of the genetics of *Paratettix* the decision must remain in doubt, and I am willing to admit that there may here be something exceptional.

Apart from exceptions probably capable of special explanation, the quantitative mode of expression clearly and sufficiently repre-

sents a very wide range of genetic phenomena. No hypothesis whatever is as yet offered as to the nature of the factors, as to the manner by which they produce their effects, or as to the regulatory process by which, in such manifestations as those of colour-pattern, the effect is directed with more or less constancy into special regions. For this last phenomenon I have no doubt a simple mechanical cause will hereafter be discovered, and it will then seem no more remarkable that the pigment of the Dutch or of the Himalayan Rabbit should occupy their respective positions, than that the shapes assumed by floating drops of oil should be influenced by the constitution of the fluid on which they rest, or their positions of rest by the shape of the vessel.

Johannsen has recently discussed again the conception of units and taken views somewhat different from those to which I have inclined. In so far as his criticisms lead to negative conclusions, the difference between us is, I suspect, verbal only. The term "unit-character," to which Morgan also takes prominent exception, means of course a character brought into being by the operation of an element or factor which segregates as a unit. No confusion is introduced by the abbreviation. By associating that term with the notion of "unit-parts" Johannsen implies that our present ideas are merely an amendment of those involved in the old debate on "præ-formation or Epigenesis," whereas modern genetics has the special merit of obviating the need for such discussions. He adds: "Nowadays each of Bateson's allelomorphs are [is] not regarded as a kind of germ ('*Anlage*') for a corresponding 'unit-character'." I cannot imagine how anyone should at any time have so regarded them. For me they have always been simply ingredients, contributions to the collective stock which makes up the organism. Nor can I agree with Johannsen when he says: "The worst of all these relics is probably the expression *Transmission*, where no transmission exists but where continuity is found." If we had to re-make our language, we might with slightly greater precision say that a unit was *de*-mitted, but to say that it is transmitted or sent through to the offspring introduces no wrong metaphor, and accords well with the quantitative representation of units. One of the most valuable principles to which Mendelism introduces us is the fact that an organism can only pass on what it itself possesses.

In one of their contentions my critics are right. The course of the evidence may convince us that of each allelomorphic pair one is

positive and the other negative, but we have not yet the means of distinguishing with complete certainty which is the positive and which the negative. Ten years ago I called attention to this paradox[1]. With sufficient perversity the albino may be symbolically represented as the positive, and the normal as the negative. If R is a factor which when homozygous inhibits colour, then the albino is RR and the coloured forms are either Rr or rr. If dominance is complete I suppose few would favour this mode of representation, since we all but know that it is nonsense; but when dominance is, as often, imperfect, I grant that we have no satisfactory criterion for distinguishing positive from negative and can only guess from analogies. I may guess that the white element in the Blue Andalusian is a peculiar dominant white, partially inhibiting the black, but I am not at all sure it is not a peculiar recessive white, diluting the black: and we have all seen plenty of examples, where such characters as leaf-shape are involved, in which we cannot yet hazard a surmise, or attempt to allot the positive and the negative parts. But the appeal to this present imperfection of knowledge does not touch the essence of the problem, and the Presence-and-Absence or quantitative conception is in such complete harmony with the tenour of the evidence, that I have no serious doubts of its correctness.

Mohr and Wriedt[2] have raised a question of interest at this point. Discussing a peculiar brachydactyly they suggest that the organism homozygous for the abnormality may be non-viable, and incline to regard one of their records as exemplifying that condition. Now if one dose of normality were needed to keep the organism alive we might, without straining the evidence, regard it as an inhibitor, the *absence* of which had, in double dose, a lethal effect. Surprise has often been expressed that human abnormalities should in such a large number of instances descend as dominants. Nothing comparable is known for any other organism. To interpret all these as examples of the addition of new positive elements is difficult. On the lines of the new suggestion a not unacceptable alternative is provided.

The *Drosophila* workers having rejected the whole scheme, on general grounds which, as I have argued, seem insufficient, claim further that some of their special experiences are not reconcilable with the Presence-and-Absence hypothesis. Without intimate acquaintance with the phenomena I cannot form an independent

[1] *Pres. Address to Brit. Ass.*, Melbourne, 1914, pp. 17–18.
[2] *Carn. Inst. Pub.* 1919, No. 295.

opinion as to the validity of these objections. Apart however from them, in a wide survey of the genetics of plants and animals I find nothing very seriously conflicting with the quantitative representation of Mendelian distinctions.

In the very remarkable paper of Bridges[1] describing triploid intersexes in *Drosophila*, a new and attractive conception is introduced which should lead to further developments. According to this system, sex is determined by a *balance* between the powers of the *X*-chromosome and those of the autosomes, especially that of the IVth chromosome. A graduated series is thus constructed, ranging from a form with 3 *X*-chromosomes and 2 sets of autosomes—which is called a "super-female"—down to a "super-male" with a single *X*-chromosome and 3 sets of autosomes. If I might call the bottom term an *infra*-male, I should regard the series as an excellent example of the quantitative system of representation.

The existence of such a series renews the hope that a way may yet be found of bringing sex-determination by a "heterogametic" male (*Drosophila*, man, etc.) into harmony with that by "heterogametic" females (moths, birds). Since in *Drosophila*, etc., female is *XX* and male *X*, if in the moth female were *X* and male zero, the whole would form one quantitative series. From this simple account we are barred, not merely by the observations of Seiler that the male moth has two visible *X*'s, but by the universal experience that in moths and birds the male may be homozygous in sex-linked factors, and thus, by inference, in *X*-chromosomes. I know no other so serious objection to the quantitative hypothesis. The two types of sex-determination, however, constitute an outstanding puzzle, with which no theory of evolution has yet satisfactorily coped.

2. The Moment of Segregation. Anisogeny

The work of the Columbia school has shown beyond possibility of doubt that in animals the reduction-division must be the moment at which segregation in respect of Mendelian factors is usually effected. These—the transferable factors—must be in some way associated with the chromosomes. We have no idea what the nature of that association may be, but that it is a reality the discoveries built on the facts of non-disjunction sufficiently prove. Especially convincing

[1] "The Origin of Variations in Sexual and Sex-linked Characters," *Amer. Nat.* LVI, 1922, p. 51; and *Sci.* N.S. LIV, Sept. 16, 1921. A fuller development of this conception of "balance" will be found in the new paper by Bridges, *Amer. Nat.* LIX, 1925, p. 127.

are the preparations proving that certain features in *Drosophila* appear exclusively in those insects which have the IVth chromosome haploid, and that other distinctions occur regularly where the same chromosome is triploid. The demonstrations of those facts which Dr Bridges was good enough to give me in December, 1921, would dispose of the most inveterate scepticism.

But if we press for a more exact account of the nature of the association subsisting between factor and chromosome, no answer is forthcoming. That the particles of which the chromosomes consist should by virtue of various chemical composition possess these highly varied factorial powers, appears in an extreme degree improbable. As to the mechanism by which crossing-over might be effected, we have scarcely any plausible suggestion, and none which is in certain accord with cytological observation. Further discussion at the present stage is unfruitful. We await a fresh light.

The fact that the chromosomes are observed in the cell-divisions of tissue-cultures to disappear[1] altogether after telophase and to pass into solution, makes the application of the conventional idea increasingly difficult, though providing unlimited possibilities in fresh directions. If the genes are, or are attached to, particles of material grouped in a more or less permanent arrangement in the chromosomes, and if these particles return to their serial places after dissolution of the chromosomes, in preparation for the next mitosis, we may have to do with a behaviour of matter hitherto, I believe, unrecognised by physicists.

Apart from difficulties of a fundamental character, we meet with various indications, which though capable of a logical and formal reconciliation with the simple chromosome theory, are not quite readily explained away. As measured by the frequency of cross-overs the assignment of factors to definite positions is open to errors of many kinds and unfortunately at present we have no other method of investigating this problem.

As various evidence has shown (especially that of Mavor[2], working with X-rays), the number of cross-overs may be influenced from without, and whether the change is due to alteration in the position of the gene, or to disturbance of the mechanism of crossing-over, cannot be clearly distinguished. The experience of all geneticists is that some

[1] Strangeways, T. S. P., *Tissue Culture in Relation to Growth and Differentiation*, Cambridge, 1924.

[2] Mavor, J. W., *Proc. Soc. Exp. Biol. and Med.* xx, 1923, p. 335.

cross-over values are liable to great fluctuation, and the linkage of one factor with another may even prove to be a transient association, as Hammarlund saw in *Pisum*. He fertilised a double recessive (white flowers, yellow pods) with pollen from a double dominant (purple flowers, green pods) and raised 10 F_1 plants whose offspring gave a normal 9 : 3 : 3 : 1, with no linkage. Using as polleniser a double dominant, sister to that used in the first series, he raised 13 F_1 plants which showed a clear 63 : 1 linkage; and with the same pair of parents crossed reciprocally he raised 19 more F_1 which showed the same linkage[1]. I suppose these facts must be taken to show that one or other of the two genes which were in the same chromosome in one plant, were in different chromosomes in its sister. No one is in a position to deny the possibility, but it opens up a bewildering prospect.

In our work on the linkage of *Primula sinensis*, another unaccountable fact has appeared. In this hermaphrodite plant, the values for certain linkages differ considerably on the male and female sides. The extreme cases are as follows:

	Observed linkage		Percentage of cross-overs	
	Female	Male	Female	Male
Short style and blue in flower	12·2 : 1	7 : 1	7·5	12·5
Green stigma, light leaf	29·6 : 1	52·4 : 1	3·2	1·8

Any attempt to account for the pairing of these allelomorphic elements in the conjugation of the parental chromosomes encounters serious difficulties—the more so since the closer linkage is in the first instance on the female side, and in the second on the male. All four factors are in the same linkage-series.

The *Drosophila* workers alone can decide whether in the course of their experience analogous complications have arisen, but provision for much elasticity and emendation is needed to bring the chromosome theory into accord with the facts of plant genetics.

On a wider survey also of the facts of heredity we see indications that the conception of linkage provided by the chromosome theory, though probably containing an essential truth, is in some important respect imperfect. We have, for example, to recognise that in segregation blocks of characters may exhibit a coherence not readily attributable to that random collocation of genes in single chromosomes, which is the only type of linkage contemplated by the theory.

[1] *Hereditas*, IV, 1923, p. 235.

An exceptionally striking instance of this phenomenon was seen by Engledow in families derived from the cross Polish wheat × Kubanka[1]. He enumerates ten characters of the grains and glumes which thus cohere and are as he terms them "inseparables." They may no doubt, as he remarks, be all controlled by one factor, and for some, as for instance the lengths of grain and glume, this may easily be supposed. Nevertheless others, such as the ribbing of the glume, its consistency, and the numbers and length of the hairs at its apex, would naturally be regarded as independent. It may be suggested with plausibility that this segregation in blocks is to be attributed to the fact that the cross in question was made between parents which have some claims to be regarded as real species, and that the association of characters may be due to an association of particular chromosomes. The evidence should be watched for signs of any such behaviour as a characteristic of species crosses. If established as of at all frequent occurrence, the generalisation might be of much significance[2]. Meanwhile, so far as *numbers* of chromosomes are concerned, it may be remarked that Kubanka and Polish are alike, with $n = 14$[3].

When a genetic analysis of human characteristics becomes possible I have no doubt that many such examples will appear. What we know of the transmission of family likenesses both in physical and mental attributes is not easily consistent with the theory of random assortment in chromosome groups. In controlling the form of the orbit, of the alæ, and of the lips, features upon which human resemblance especially depends, we cannot doubt that countless genetic elements take part. That this is true is proved by the easily observed fact of recombination, and yet strong likenesses extending to features of all kinds shared by many members of the same family groups are to be observed every day. This is scarcely consistent with the supposition that the elements co-operating to produce these miscellaneous effects are wholly independent in their transmission; but we have equal

[1] *Journ. Gen.* x, 1920, p. 124.

[2] W. H. Gates has lately published a preliminary account of crosses between Japanese waltzing mice and house mice in which the characters similarly segregate often in blocks. Evidence is added indicating that the Japanese are *Mus wagneri*, regarded as a distinct species. *Proc. Nat. Ac. Sci.* xi, 1925, p. 165.

[3] In plant-sports somatic segregation by blocks is occasionally seen. Sageret (*Ann. de la Soc. d'Hort. de Paris*, ii, 1828, Livre 7, p. 159) describes in detail such an example in a melon which bore two fruits differing from each other in several respects of structure, colour and flavour.

difficulty in interpreting these extensive associations as merely manifestations of chromosome linkage.

If referred to chromosomes, these associations of factors suggest rather a partial grouping of particular chromosomes than a collocation of factors within individual chromosomes, but the consequences of the two processes may readily be confused.

Goodspeed and Clausen's *Nicotiana* crosses are very suggestive of such association. Reciprocal crosses between six different varieties of *N. tabacum* and *N. sylvestris* gave F_1 resembling the particular *tabacum* variety used. These F_1 plants had sterile pollen, but the female side could be back-crossed with the parental species. With *sylvestris* father they gave two classes of offspring: (1) aberrant plants which were almost sterile and gave no seed when selfed; and (2) plants partially fertile closely approaching *sylvestris*, which on selfing in successive generations soon produced a fully fertile line not distinguishable from *sylvestris*[1].

The converse combination, $F_1 \times$ *tabacum*, gave three classes: (1) aberrant nearly sterile forms producing no seed when selfed; (2) forms like *tabacum*, also almost sterile; (3) plants partially fertile, resembling *tabacum*, which on selfing resulted in a fertile strain like the original *tabacum* in appearance. In a recent paper Goodspeed gives an account of the cytology of these hybrids. *Sylvestris* has $n = 12$ and *tabacum* $n = 24$. In F_1 therefore twelve chromosomes go unpaired. Here therefore the fact that the fertile derivatives are those which most closely reproduce the parental types is interpreted by the observers as meaning that only a few of the chromosome combinations are sufficiently harmonious to be effective, and that these are approximately those which constituted the original species. The comparative fertility of the female side of F_1 is the chief obstacle to this interpretation, but if not unduly pressed, the scheme may be accepted as being in general accord with probability.

Somatic Segregation

Though we can no longer doubt that segregation is, perhaps by more than one process, commonly effected at the reduction-division, evidence steadily accumulates showing that at least in plants of many kinds comparable segregations occur in somatic divisions also. When we first knew that linkage was an expression of parental association of characters, Punnett and I suggested that by some process of vege-

[1] *Amer. Nat.* LI, 1917, p. 31.

tative reduplication, the cells bearing the parental as opposed to the cross-over combinations became more numerous. The chromosome theory obviously provided an alternative account which we admit to be so much more probable that the conception of reduplication fades inevitably into the background. Whether reduplication ever happens at all as originally suggested is doubtful. Such a consequence might not improbably ensue in the growth and multiplication of material like the germinal tissues, *commonly devoid of axes of symmetry*, but admittedly we cannot point to any observation which is conclusive. I notice, however, that both Nilsson-Ehle in Wheats, and Heribert-Nilsson in *Œnothera* have met with phenomena which they incline to regard as examples of reduplication.

Anisogeny

Breeding tests have proved that in heterozygous plants of many kinds the pollen and ovules are unlike in the genetical contributions which they make to the composition of the next generation. The first example was discovered in Miss Saunders's experiments on single "double-throwing" Stock (*Matthiola*), the pollen of which bears exclusively the recessive doubleness, whereas the ovules are mixed, some bearing singleness, others the recessive. The same rule was soon ascertained to hold good of the white and cream plastids in the white race which continually throws creams, and again the pollen bore exclusively the recessive. This phenomenon is so common and is the subject of such constant reference that a special designation for it is required. We have sometimes spoken of such distributions as "unilateral," as opposed to the ordinary or "ambilateral" distribution in which both sides, male and female, equally participate. These terms are open to certain objections, especially on the ground that inasmuch as the female side generally, perhaps always, carries a mixture, the distribution is not strictly one-sided. The choice of a term is rendered difficult from the absence of agreement as to the physiological nature of the distinction between the two sides. I should wish to express the fact that there has been a *separation*, such that the one allelomorph passes to one side wholly or predominantly. Those, however, who regard all genetic segregation as effected at reduction, have put forward alternative interpretations. For them the appearance of separation at some somatic division is spurious; and the absence, for instance, of singleness in the pollen of *Begonia Davisii*, is taken to show not that the singleness is not represented among the grains, but

that the grains bearing it are by some unknown process rendered inoperative. Some writers use the expression "heterogametic" in application to these plants; but the term (as well as "heterogamic") is already in general use both in zoology and botany, with several distinct meanings, of which perhaps the most usual and important is in application to the heterozygous sex of animals—the male or the female, as the case may be. For this use, in which it is entirely appropriate, the term "heterogametic" might be maintained exclusively. Pending clear evidence as to the nature of the phenomenon, it may perhaps be best described as *anisogeny*, a term which merely declares that the contributions of the two sexes are unequal, in contrast with the normal or *isogenous* condition in which they are alike.

Besides those in the Stock, already mentioned, the most familiar examples are those gyno-diœcious plants in which the females fertilised by pollen of hermaphrodites give entirely or predominantly females. This was, I believe, first recognised by Correns, though no interpretation was at that time offered. In collaboration with Miss A. E. Gairdner, I have investigated a simple and particularly instructive example of anisogeny in *Flax*. Ordinary flaxes, both fibre and oil varieties, are regularly hermaphrodite. A peculiar dwarf form which appeared here spontaneously[1], is similarly hermaphrodite, but fertilised by any fibre flax it gives in F_2 an ordinary recessive, characterised by male sterility, complete or less often partial. Fertilised by fibre flaxes, these recessives give nothing but similar male steriles, whereas, fertilised by pollen of the dwarf, they give all hermaphrodites in F_1, which in F_2 give a normal 3 hermaphrodites : 1 sterile.

The obvious and most simple interpretation of these facts is that in the fibre flaxes the element which determines hermaphroditism passes into the female side of the plant, leaving the pollen devoid of this factor.

Analogous evidence has accumulated from various gyno-diœcious plants, but flax is peculiar in that, although the heterozygous combination in the normal flax segregates upon the anisogenous plan, nevertheless if the hermaphrodite factor be introduced from the dwarf variety, the heterozygote is isogenous and a normal 3 : 1 results. I can suggest no reason for this distinction.

In *Campanula carpatica* Miss Pellew has found that anisogeny

[1] We have never succeeded in tracing this variety. It is a *usitatissimum* and perhaps is somewhere cultivated for oil (see *Journ. Gen.* XI, 1921, p. 269).

governs not only the anther-development, but also, less completely, the factor for blue colour as opposed to white.

In none of these examples do I see any difficulty in attributing the anisogeny to some somatic segregation occurring in the course of the development of the flower.

The advocates of gametogenesis as the exclusive seat of segregation have made several alternative suggestions, invoking lethal factors acting either on gametes or on special zygotic combinations, differential properties of gametes of special constitution affecting their germinative or fertilising powers, and similar discriminating influences; but so far I am not aware of any positive or material evidence pointing in these directions. Admittedly no decision can be made with complete certainty as yet, and in the next examples complications exist which have not yet been elucidated. In *Begonia*, as in *Matthiola*, anisogeny in respect of double flowers[1] is met with. Most remarkable in this respect is the case of *Begonia Davisii*, a wild species which, though breeding true to singleness, gives exclusively double flowers when its pollen is used to fertilise the female flowers of doubles[2]. Definite anisogeny has been found to exist in *Begonia semperflorens*[3], affecting the distinction between red and pink flowers. Pink is dominant, and commonly the male side of the heterozygote gives 1 pink : 2 red, whereas the female side gives equality. Both these proportions have been determined by back-crossing on a large scale, but for some reason unknown, the heterozygotes *selfed* have given approximate equality (2782 pink, 2536 red; or 1·1 : 1) instead of the arithmetical expectation 2 pink : 1 red. Such a fact may be construed as an indication of selective action. In connection with it should be mentioned the production of a small but significant proportion of slightly petalodic

[1] Petunia has been sometimes quoted in this connection, but, as now appears, in error. Doubles are functionally male only, having no ovaries. They are always raised by fertilising singles with the pollen of doubles. A mixture of singles and doubles results, of which the singles breed true. Miss Saunders, on the analogy of Stocks, took the doubles to be recessive, but, as Frl. von Ubisch pointed out, the double may more simply be taken to be a heterozygous *dominant*, like the ordinary double *Carnation*, on which interpretation no problem arises (*Zeits. f. Botanik*, XV).

[2] W. Bateson and Ida Sutton, *Journ. Gen.* VIII, 1919, p. 199. During the past 6 years these experiments have been greatly extended by Miss de Winton. Not merely has the original *Davisii* this anisogenous distribution, but singles derived from its female side successively fertilised by doubles continue to behave in the same way for several generations unchanged.

[3] This is a subject on which I have been engaged for several years in collaboration with Miss D. de Winton.

plants in the cross *Begonia Davisii* ♀ × double ♂. Since *B. Davisii*, itself fertilised by its own pollen, gives no double flowers, and, as we have just seen, its pollen judged by back-crosses must be supposed to bear doubleness exclusively, the origin of these petalodics is problematical and may conceivably indicate that the eggs producing them do not, for some reason, take part in the normal descent of the species by selfing or *inter se* fertilisation[1]. What the meaning of these unconformable results may be, we cannot say, but they must be mentioned as in some degree throwing doubt on the simple interpretation of anisogeny to which I incline.

A feature which, as cases multiply, assumes a certain significance is the fact that in all the examples of simple anisogeny yet discovered in plants the peculiar property of the pollen is to carry the recessive. Petunia used to be quoted as an instance to the contrary, but as remarked, that interpretation has now lapsed (p. 422, note). Attempts to build up an anisogenous plant in which the properties of the male and female sides should be reversed have not, so far as I know, been as yet successful.

Among the Œnotheras, as de Vries first showed, anisogeny prevails extensively. It is there combined with the further complication that the characters may be associated in groups or blocks which are difficult to interpret as examples of ordinary linkage. The further investigations of Renner and other *Œnothera* specialists have greatly increased our knowledge of this subject, but the facts are so complex that a general idea of the genetics of these plants is all that those unfamiliar with the material can form. In the abundance of dead pollen grains so commonly seen in them we have here palpable evidence of special complications, added to which, lethal zygotic combinations almost certainly play a considerable part. For these reasons we can scarcely appeal to the Œnotheras as elucidating the anisogeny of plants in which none of these disturbing elements have as yet been demonstrated.

Among the phenomena which Miss Irma Andersson[2] has observed in studying the genetics of variegated ferns are several which illustrate a segregation among somatic cells in respect of the condition of the

[1] We cannot easily attribute the petalodics to some more extreme doubleness brought in by the double used as male, for *Davisii* itself, used as a male, is evidently genetically a thorough double. Nevertheless that possible interpretation must be remembered.

[2] See *Journ. Gen.* XIII, 1923. The work on *Scolopendrium* is still unfinished.

chloroplasts. In one example especially the behaviour offers a remarkable analogy to what is here called anisogeny. Variegated *Scolopendrium*, characterised by bands of pale yellowish green, produces from its spores prothallia either fully green or in various shades of paler green. The fully green prothallia stay green and give rise to ferns which are wholly green and breed true. The pale prothallia rarely range up to green, and when bred together give variegated ferns only, no greens and no whites. But the most curious feature in this case is that the 64 spores in any one sporangium are commonly not mixed, but exclusively of the one kind or the other, giving rise either to all green or all pale prothallia. Since here there can be no question of missing spores, the conclusion that segregation happens in somatic tissue, long before spore-formation, is inevitable. The character of the sporangia is, moreover, not determined by that of the area on which they stood, but was independent of it.

3. Rogue Peas and Anisogeny

The genetics of rogues among culinary peas present two special features, of which one is so far without any known parallel. The facts are, in outline, that rogues arise spontaneously as a small percentage in many, probably all, modern strains of peas. The chief characteristics are *pointed* leaflets, an upward *curve* in the pods, and *reduction in size* of the appendicular parts. In most varieties the rogues are approximately uniform. Gradus is exceptional in having intermediates as well as the ordinary rogues. Rogues always breed true to their character. The Gradus intermediates throw *chiefly* rogues, with a few intermediates and an occasional type. Crosses between types and rogues of the same variety[1], however made, give F_1 in their early stages intermediate, but turning at or below the first flowers into rogues, producing, that is to say, rogue-like parts at and above these levels. Self-fertilised, these plants breed permanently true to rogue. We have been engaged on this investigation for some twelve years. In our opinion all we have seen is consistent with the supposition that the type-element is left behind in the lower parts of the cross-bred plant. In the Gradus intermediates the type-element commonly disappears more gradually. The change is generally marked at the level of the first flower, and progresses rapidly, as successive nodes

[1] In Sugar-pea crosses the intermediate nature may persist longer, so that the plants then pass for intermediates, and the same is occasionally the case in F_1 made from the cross of types and rogues belonging to very distinct varieties.

are formed, so that the upper part of the plant is thorough rogue. Less often, the transformation is delayed and occasionally the pointed leaves do not definitely appear at all, though the pods curve. The genetical properties of these two classes of intermediates are different. The first group, as stated above, throw mostly rogues, with a few of the higher kinds; the incompletely transformed throw mostly types and high intermediates, but a percentage of true rogues greater than that thrown by real types. The progressive transformation at successively higher levels agrees well with our interpretation.

The genetical behaviour is also confirmatory. We have found by observing the produce of the several nodes self-fertilised, that the few types which the pointed intermediates give, come predominantly from the lower nodes. Above these there is an ordinal decline in the proportion of types produced at successive nodes. Just as the somatic character progressively changes, so—though the correspondence is irregular—the genetical properties follow. We have never seen any similar progression in the genetical behaviour of those intermediates which do not acquire pointed leaves. The rogues which they throw do not come with any special frequency from the higher levels, but are distributed uniformly among the pods, just as from the somatic appearance of the parents might be expected.

Finally, the pointed intermediates show also a progressive anisogeny. By reciprocal crossing between their successive flowers and types it was proved that the increase in rogue-production is very much more rapid on the male than on the female side. Miss Pellew has lately shown (unpublished) that even in an F_1 from type × rogue (from a distinct variety), the lowest flowers fertilised by pollen of type may produce actual *types*. Nothing comparable has ever resulted from the use of F_1 pollen.

This series of facts taken together amounts nearly to proof that the somatic divisions result in the exclusion of a parental contribution, and that this process is orderly. By what cytological changes the result is accomplished we cannot surmise. It should however be remarked that in the organs of F_1 plants mosaicism occasionally exists—especially leaves having leaflets or half-leaflets of type and rogue associated; and that in Gradus intermediates these mosaic combinations are frequent, more particularly in leaves at the lower flowering nodes. We incline therefore to suppose, not so much that any successive cell-divisions result in progressive loss of the type-elements—which is most difficult to conceive—as that at some

divisions, perhaps several, especially those associated with flower-formation, this element is dropped out. To obtain positive cytological evidence on such a point seems almost impossible. All that we know at present is that types and rogues do not differ in chromosome-number, both having $n = 7$.

4. Chimæras, Regular and Irregular

Ever since Baur demonstrated the fact that variegated periclinals give offspring of the type present in the sub-epidermal layer the great significance of this class of plants for genetical study has been recognised. Whatever be the true account of their germinal origin, here are plain instances in which the somatic differentiation can be often demonstrated to be a true indication of genetic potentiality. The application of such evidence to the general theory of heredity is open to the obvious objection that since the distinction between the layers is one of plastid physiology, the segregation of which these distinctions are the result may be wholly operating with the plastids themselves, whereas the segregations determining ordinary heredity operate with other elements of the cell, notably the chromosomes. Variegation, however, may come about from any of several dissimilar causes. It may be due to the inheritance of defective plastids or it may be a consequence, as Baur first showed, of the presence of a positive bleaching factor. This latter class of variegation is transmitted in ordinary Mendelian fashion; and though in none of the periclinal chimæras where *white* is combined with green has the distinction yet been shown to belong to the Mendelian group, nevertheless those periclinals which have an *aurea* skin over a green core are a clear illustration of a somatic segregation in respect of the Mendelian bleaching factor. As Noack has seen and we here also have found, such periclinals breed as ordinary heterozygotes; and that the bleaching factor is restricted to the skin is proved by the fact that the green core, when it emerges, breeds as an ordinary green. Therefore a Mendelian element is, by some process of somatic segregation, relegated to the skin. Evidence of the existence of certain analogous periclinals will be next considered. In dealing with variegation of the green parts the distinction between the outer and inner layers is plain to the eye on simple inspection, but by raising adventitious buds proof may sometimes be obtained that plants, not ostensibly chimæras, do in fact contain a core having distinct characteristics.

In previous papers[1] I have described some of these in *Bouvardia* and in Pelargoniums of the fancy or "Regal" classes. The adventitious buds were in these instances obtained by growing pieces of roots removed from the parent plants. By this method the composition of a considerable number of varieties has been tested and in a few of them positive results have again been obtained.

In Bouvardias, Oriental Poppies and Phloxes root-propagation is so easy that the method is, or was, in common use among gardeners for commercial purposes. With other plants the amputated roots often rot without budding. Following the suggestion of Mr Stewart, of Edinburgh Botanic Garden, we tried lifting the plants so that the roots lay partially above the soil, and had some better success. This led to the bolder step of lifting the plants so that the roots were wholly out of the ground, cutting off the tops together a few inches above the collar, and keeping the whole damp under hand-lights on the fibre-bed in the stove house. For convenience of handling the whole beheaded plant is inverted and stuck stem downwards into a pot of soil, with the washed roots in the air. Frequent syringing gives sufficient water if the plants are kept close and moist. With many Pelargoniums, both Zonal and fancy, Nicotianas and various other plants, abundance of buds sometimes arise on the exposed roots. These root-buds, when they acquire a few leaves, are eventually cut off and encouraged to strike. At this stage many are lost, but a good proportion eventually root and become plants.

Bouvardia. As previously published, Bridesmaid, pinkish white double, has uniformly given *red* (Hogarth) double from its roots. These propagated again from roots have given their own type, but as an exception once, a *single* red. This latter has always given its own type only from its roots.

Vulcan, deep red, besides many like itself, gave once a rose pink.

Princess of Wales, a pinkish white single, the same colour as Bridesmaid, has, like it, given red singles from roots. At first I supposed that Princess of Wales must be merely a single Bridesmaid, but the leaves of Princess of Wales and those of its ordinary root-"sport" are glabrous, whereas those of Bridesmaid and Hogarth are covered with short hairs. Since the anthocyanin is, as usual, confined to the epidermis of the petals, periclinal heterogeneity would not be *à priori* expected to be an attribute of any particular colour, and the coincidence is therefore remarkable.

[1] *Journ. Gen.* VI, 1916, and XI, 1921. [This vol. p. 264 and p. 321.]

Pelargonium. As already published, the named varieties of Fancy Pelargoniums known as Pearl, Mrs Gordon and Escot have all given distinct forms from their root-cuttings, the distinction in each case being primarily in flower colour. The flowers of Escot's root are in addition flat and considerably larger than the flowers of the type, the petals of which are slightly rolled back. Similarly from Duchess of Portland, a *whitish* salmon-scarlet, the root gives a densely coloured flower of the same pigmentation, with guide-marks of increased size.

In three Zonals the roots have given plants with flowers differing in the development of the reproductive organs and in other respects. Salmon-fringed, in which the type has petals laciniated, with the female parts undeveloped, gives a normally hermaphrodite plant with normal petals from its roots. The leaves are also flat, not crumpled as those of the parent plant are.

Double New Life has very peculiar double flowers, female only, and devoid of anthers. Mr R. J. Chittenden has found it to give a normal hermaphrodite Zonal from its roots.

Kleiner Liebling, with minute, white-edged petals and no anthers, also gives a normal hermaphrodite with flowers of ordinary size from its roots. In contrast to these positive results, one or more root-cuttings have been raised from 56 named types (miscellaneous fancy[1], Zonal, or scented-leaved) without giving anything different from the parent plants.

In all the examples hitherto given the inner component may be regarded with some plausibility as differing from the outer in the possession of a dominant. The only instances I have seen in which the converse arrangement appears to exist are certain purples or magentas. For example, Don Juan, a full magenta Fancy Pelargonium, was first known to me as a large plant at Kew bearing two kinds of flowers, some magenta, some crimson red, with others patchworks of both colours. When separately propagated the roots of the red form have always given reds, whereas the only two root-cuttings raised from the magenta have both been reds. Red may therefore be taken to be the inner component, and judging from analogy is probably the recessive The red Don Juan is liable to have occasional flakes of magenta, though the magenta has never in our experience had flakes of red. Whether this point is of significance I cannot say, but comparable instances have occurred with other reds and magentas in *Pelargonium*.

[1] Many names, such as fancy, show, regal, etc., are applied to the large-flowered Pelargoniums, but I have not attempted to distinguish these.

Clorinda, for example, is a pink scented-leaved variety, which is also liable to have mauve flakes. From it we have raised a mauve sport by propagating a shoot which no doubt arose from a growing point in a mauve area. Root-cuttings from both the mauve and the pink give pinks only, though, as in Don Juan, these pinks are liable again to have mauve flakes[1]. Rollisson's Unique is in all probability a comparable example, but beyond seeing purple trusses and flakes arising on the original red I have not yet tested it.

Besides these strikingly distinct plants which arise with some constancy (so far as observed) from roots of their respective types, a group of three root-cuttings from one Fancy seedling, bred here, contained two like the parent and one quite distinct in flower-colour. Evidently, therefore, uniformity in the distribution of characters among the somatic parts even of a single plant must not always be expected, and the analogy of chlorophyll distribution in the variegated plants is probably a true guide. Just as in the variegated plants rearrangements of the green and white parts are effected, sometimes with great frequency, by the divisions of the growing point, one or other of the components being often excluded altogether, so may similar changes happen in these periclinals. It is to be remembered also that in plants like Pelargoniums, which are continually propagated by cuttings, the original root is no longer present, and there is no certainty that the plerome of the stem is of the same genetic constitution as the original root. Experience of variegated plants shows also that it is from the *bases* of propagated shoots that stems showing new combinations especially appear, though *why* novelties should arise with special frequency in that position we do not know.

Of the varieties mentioned as having given novelties from their roots, Pearl, Salmon-fringed and Double New Life have shown more or less frequent sports or mosaics of the inner component, but neither Mrs Gordon, nor Escot, nor their root-cuttings, have ever given a spontaneous sport in our experience. These various degrees of constancy are exactly what we have observed in the behaviour of the several variegated types.

Attempts have been frequently made to raise new plants from the *leaves* of Pelargoniums. Most commonly roots are formed from the

[1] The mauve form of Clorinda is known to horticulture as Joan. Whether the pink is the older form I do not know, but Don Juan traditionally arose as a sport of Lily Krumholz, which presumably was the red variety, though spoken of in catalogues as "rosy magenta."

callus at the base of the petiole, and such rooted leaves may live for months or even years without the production of any bud. From Escot on three occasions leaves have given buds which developed into plants. From such adventitious buds we expect the inner component to appear, and from two leaves plants did arise identical with those from Escot's root. The third leaf, however, gave a curious and interesting result. *Three* several shoots arose from it. One was the normal Escot, like the parent; another was Escot's root-form; and the third was distinct from either, having the size and markings of the root-form and the ground colour of the type.

Allocation of the characters among the somatic layers is not generally possible. In such a plant as Salmon-fringed we are clearly safe in speaking of the arrangement as periclinal; but though the constant appearance of a particular type from root-cuttings must indicate that the arrangement is orderly and doubtless that the root-form is the inner component, the structure of the variegated plants warns us that we cannot tell through how much of the plant that inner component extends. Further, such evidence as that from Escot's leaves shows that some recombination may take place in regions of active meristematic growth, and suggests that the process may not be, in any simple sense, orderly.

In view of Noack's[1] studies a doubt must be expressed whether any of these plants are periclinal chimæras in the original implication of that term. We have hitherto supposed that the segregation to which the distinction between the layers is due had been determined in embryonic development, when the plerome was defined from the periblem. Noack comes to the conclusion that the outer and inner components owe their distinction to segregation continually recurring in meristematic divisions of the growing "labile" tissues. To decide between these two possibilities is not easy, but undoubtedly Noack's view has the merit that it somewhat diminishes the difficulty of imagining a mechanism by which changes in the relative positions of the layers can occur during vegetative growth. Such changes are sometimes frequent, as in L'Élégante, an ivy-leaved Pelargonium commonly white-over-green, but always liable to produce green-over-white parts. The reversal may not infrequently occur in such a way that part of a leaf may show the white *outside*, the rest of the same leaf being green-over-white. In salmon-fringed Pelargonium,

[1] *Verh. Phys. Med. Ges.* Würzburg, 1924, N.F. XLIX, p. 45, and *ibid.* L, 1925, p. 47, and *Jahrb. wiss. Bot.* LXI, 1922.

flowers are often patchworks of the outer and inner components, and on Kleiner Liebling we lately had a truss bearing several sterile flowers of the type on one side, and on the other side fertile flowers showing the character of the inner component in various degrees of development. In comment the similar production of patchworks in *Cytisus Adami* and the *Cratægo-Mespilus* combinations may certainly be appealed to, but we know so little of the real nature of those plants that testimony derived from them has as yet no final validity.

Doubt may also be felt as to whether the root is in reality a periclinal combination in any of these plants. Up to the present we have no proof that the outer component extends into it. Sometimes it may perhaps do so, but the distribution of the green parts at least in Freak-of-Nature Pelargonium and in the variegated *Spiræa ulmaria*[1] suggests that the root is wholly albinotic in those plants, and probably the same may be true of real periclinals.

Bud-sports have usually been regarded as evidence of a sporadic and fortuitous variation, there and then occurring in a somatic division. Question now arises as to whether they are not in reality the emergence of a constituent congenitally or at least long previously present in the plant. In practice, doubtless, both possibilities are realised, but I anticipate that in general, sporadic and spontaneous bud-sporting, as popularly conceived, is a very rare and exceptional event.

The genetical significance of somatic sports, whether sporadically emerging or arising from adventitious buds however produced, can only be determined by breeding. *Bouvardia* and *Pelargonium*, with which I have been specially concerned, are shy breeders and unsuitable for such determinations. As Baur showed in regard to the chimæras of variegation and as Winkler's "graft-hybrids" between Tomato and *Solanum nigrum* also demonstrated, the genetic possibilities are those of the sub-epidermal layer.

Clausen and Goodspeed[2] have described two most interesting bud-sports in cross-bred *Nicotiana tabacum*. In regard to one of these the evidence was exceptionally complete. The plant was raised as F_1 from *N. purpurea* (carmine), fertilised by Cuba variety (white). F_1 is normally carmine, but one plant produced a pink-flowered sector. Both parts, the carmine and the pink, were in genetical composition qualitatively identical, giving carmines, pinks, and whites in some-

[1] For figures of these plants see *Journ. Gen.* XI, 1921, Pl. XIV [this vol. Pl. XV], figs. 2 and 3; XVI, 1925, Pl. IV.

[2] *Genetics*, VIII, 1923, p. 97.

what irregular ratios. Each sector was then established on its own roots, after which the roots were propagated. The root-cuttings from the pink sector came carmine, showing that the deviation to pink was due to somatic variation affecting the epidermis only, the inner component being still the same.

As to two only of the chimæras here discussed have we anything approaching evidence as to genetic constitution. The first is the Salmon-fringed Zonal Pelargonium. The outside of this plant is functionally male only and the petals are laciniated. Chittenden, using its pollen, was successful in fertilising the eggs of the inner component, and from the normal F_1 plants produced, raised F_2. All the F_1 were normal and on being again bred with their own pollen gave a small F_2 generation, about 6, all normal and hermaphrodite, from which the inference may be drawn that the peculiar Salmon-fringed character was not introduced into the cross and was presumably a feature proper to the epidermis only[1].

The experience with Double New Life was more conclusive. Dr C. J. Bond was successful in fertilising the abnormal, external component of this variety with pollen of the inner, normal component. Chittenden repeated this, and, from the normal F_1 plants, raised about 90 plants in F_2, all normal. Hence we may conclude with some confidence that the genetical peculiarity of Double New Life, viz. the doubling and the curious whitish intercalated petals[2], is present in the epidermis only and is not carried into the sub-epidermal layer.

A close study of the phenomenon of bud-sporting in plants may be expected to extend our understanding of the nature of the process of segregation and the principles which it obeys. I notice a disposition among the advocates of the chromosome theory in its cruder form to speak of all such sports as "mutations." Such an application of this term, for example, to the manifold sports which arise through the instability of any of the numerous arrangements of the components in a variegated plant is likely to introduce confusion. A branch of a new type may arise whenever one only of the components fortuitously

[1] In the total sterility of Kleiner Liebling, and especially in the female sterility of Salmon-fringed and the male sterility of Double New Life, the two latter attributable to the presence of a special epidermis, we are reminded of Winkler's "Solanum Kœlreuterianum," which having an epidermis of *S. nigrum* over a core of *S. lycopersicum* was likewise totally sterile. Winkler, H., *Zeits. f. Botanik*, Jg. 2, Heft 1, p. 16, 1909.

[2] Mr Chittenden has pointed out reasons for supposing that these whitish petals may represent the stamens.

comes to occupy a growing point, or by various rearrangements of the components, to mention only the simplest possibilities. Mutation is a term used in a great variety of connotations by various writers. To disentangle these, even if it were possible, is a task beyond my present purpose, but in general I notice that the term is commonly employed to give an importance, even an evolutionary significance, to a change for which the common word variation is felt to be an insufficient description. To the consequences of rearrangement in a variegated plant such an expression is scarcely applicable, and in so far as a bud-sport may be merely the emergence of a pre-existing component no question of mutation arises, even though the emergent member may have distinct genetical properties.

The genetic nature of mosaics and sports is as yet obscure. In plants the problem has most commonly been investigated with reference either to variegation of the green parts, or to some feature of anthocyanin coloration manifesting similar properties. Inferences drawn from the genetics of variegation are of very doubtful application to other phenomena of heredity, for there are frequent suggestions that sometimes at least a segregation happens in respect of the plastids themselves. Moreover under the term variegation also a great diversity of conditions is included, which are alike chiefly in so far as they exhibit a common symptom. Some are simply infectious diseases, as may be seen in *Abutilon Thompsoni* and *Begonia manicata variegata*, where the variegation can be directly communicated by grafting. With these the geneticist is not immediately concerned. But even among the conditions which are unquestionably transmissible in heredity no one system of descent is followed. A few simple cases in which real variegation breeds quite true may at once be distinguished. In those with which I am personally acquainted the evidence indicates that the variegation is a simple recessive to green. The example most fully studied is the variegated *Tropæolum*[1], the leaves of which show an intimate mixture of green and albinotic tissues. This variety was formerly the subject of extensive investigation made by Miss Gairdner in Cambridge and by ourselves independently at this Institution. We found it to behave as an ordinary recessive, which could be introduced from either the female or the male side of the parentage. An account of experiments with the same

[1] For an example largely comparable though presenting certain differences, see I. Andersson, "Inheritance of Variegation in *Barbarea vulgaris*," *Journ. Gen.* XIV, 1924, p. 185.

form was lately published by Correns[1], whose experience agrees with ours. Like him we had expected green plants to arise from the self-fertilised seed of variegateds, but this never happened, variegated alone appearing. On one occasion however he had a green branch which developed on a variegated plant, and on self-fertilisation this proved to be heterozygous. Apart from this nothing exceptional occurred, and we have to recognise the paradox that the germ cell of the variegated, whether male or female, is able to transmit the mixture of green and white cells, being itself mosaic in that respect.

As to the consequences to the heterozygote of the union of a real green-bearing gamete with one devoid of green we note that no rule can be predicated. The green may behave as a dominant, as has been seen by many of the experimenters with cereals. Sometimes the maternal character exclusively appears (*e.g. Antirrhinum* white-skinned fertilised by green), but not rarely the result seems to be almost fortuitous and governed by no system. As Baur found for instance in *Pelargonium*, and Chittenden[2] has seen in similar material, an irregular somatic segregation may occur in such heterozygote tissues, such that one or other component may be wholly or partially excluded.

In our present inquiry however we are primarily concerned with the gametic product of plants which certainly contain both elements and with the manner of their segregation. Baur first called attention to the difference in genetic behaviour between the sectorial and periclinal chimæras, the former being irregular in their products, the latter regular. Variegation supplies several especially clear illustrations of this important distinction. Not merely the periclinals show a regularity in their genetic products, but some also of the variegated monocotyledons, in which an orderly striping, whether of white or green, occurs. In the periclinals we see a somatic segregation such that the genetic products agree in character with that of the foliar sub-epidermis. Similarly in striped *Chlorophytum* Collins[3] showed that it is the character of the central band of the leaf which is transmitted by the germ cells. I have seen a similar example in *Funkia*, from the narrow white-edged variety of which green seedlings exclusively result. The yellowish white-edged *Sanseviera* common in greenhouses would doubtless show the same behaviour[4].

[1] *S.B. preuss. Akad. Wiss.* VI, 1920.

[2] Chittenden, R. J., *Journ. Gen.* XVI, 1925, p. 43.

[3] Collins, E. J., *ibid.* XII, 1922, p. 1.

[4] Propagated from *leaves*, this plant gives all greens, with no lateral bands, since the bud-forming callus is developed only from the green central band.

The regularity or irregularity of the genetic behaviour of the variegated plants is evidently largely determined by the geometrical distribution of the chlorophyll character in the zygote. The geometrically regular arrangements have commonly an orderly genetic behaviour and the irregular mosaics have not. This distinction is largely independent of the nature of the character concerned. Provided that a character is *distributed according to some geometrical system governed by the normal differentiation*, it may be regularly transmitted; if the distribution shows no geometrical order, regularity in transmission is exceptional. Of this principle the genetics of variegation supply only a special case. It is probably of wide application in plant-genetics. We do not expect the anthocyanin striping of a flaked or bizarre Carnation to breed true, though the pattern of a wire-edged picotee, involving the same pigment, may be fixed.

One very remarkable example bearing on these questions, though it has other bearings also, may be introduced in this connection. *Myosotis*, "Star of Zürich," is a form having a definite white stripe down the centre of each blue petal. So far as I know its breeding had never been tested, and in horticulture it is always propagated by cuttings. Isolated in our breeding house it once produced seeds, which when sown gave exclusively plants with *white* flowers. I tried on many occasions subsequently to self-fertilise it or to make it cross with some other variety, but without success. In the open, exposed to insect pollination, it gives plenty of seeds, but these, neither in the first nor in any subsequent generation, have ever given the Zürich flower again. R. J. Chittenden at length, with considerable manipulative skill, succeeded in fertilising Star of Zürich with pollen of white flowered forms and thus raised many seedlings *all with white flowers* which have bred true. White is recessive in *Myosotis* and we thus have proof that in some way the germ cells carry the character of the white central stripe and not that of the rest of the corolla. At present I know no clear parallel to this example of a somatic difference in anthocyanin development corresponding with a genetic distinction.

Irregular Mosaics in Plants and Animals

No attempt to represent analytically the genetical behaviour of irregular mosaicism in plants has been altogether satisfactory. Confusion has arisen from the fact that a few mosaics are genetically real recessives, like the variegated *Tropæolum* mentioned above, whereas most are of an altogether different nature. As regards mosaics in

anthocyanin development I cannot recall any example in which a strain breeds true in respect of a wholly irregular distribution. Plants with irregular stripes or specks of anthocyanin are, I believe, always liable to throw self-colours with greater or less frequency.

Since usually the pure self crossed with the mosaic gives F_1 self-coloured, the relation has often been represented as that of an ordinary dominant and recessive. The subsequent history of such families is then that the self, though often throwing the mosaics, can eventually be bred true. The mosaics on the contrary behave irregularly, and with greater or less frequency throw the selfs again. This behaviour, which is evidence of some residual difficulty, is sometimes referred to "mutation," surely a misnomer.

Avoiding such expressions as genes for self-colour or genes for mosaicism, the phenomenon may, without any violation of common experience, be represented in quantitative terms. The self-colour being taken as a unit, if a complete unit be introduced on fertilisation by either gamete the result is a self. If either gamete contribute an incomplete unit to F_1, mosaics result in F_2. If both gametes contribute incomplete units the result is a mosaic soma; but by segregation in the somatic divisions of such mosaics, cells, groups of cells and tissues *may* generally be formed which contain the unit again in its entirety. We do not know enough of the mechanics of these processes to justify any choice of an analogy, but provisionally I think of the separation-out of the unit as like the running-up into drops of the globules in an emulsion, though I am unable to symbolise that conception in terms of chromosomes. The genetical behaviour seems clearly to indicate that if, as one might expect, the unit can be restored to its quantitative integrity and completeness for any somatic cell, then in plants, at all events, quantitative gametic purity can ensue[1].

I am tempted to regard Mendelian segregation in general as a process not essentially different from that which we see working in the mosaics. It is the settling-out of an element *quantitatively un-*

[1] One of the best accounts of the genetics of a mosaic plant is that lately published by Eyster ("A Genetic Analysis of Variegation," *Genetics*, IX, 1924, p. 372) on the striping of the pericarp in maize. It should be noted that this striping is a phenomenon of anthocyanin distribution, which is not what we call variegation—a term here restricted to miscellaneous chlorophyll defects. The paper supplies an abundant array of facts and especially some welcome evidence bearing on the difference in genetic behaviour between the finer and the coarser mosaics. The discussion, though employing a terminology open, as I think, to criticism, is far more illuminating than those commonly supplied.

impaired, from a combination in which, but for this property of segregation, this element would be diluted.

Admittedly the process is usually postponed to the reduction-division. Perhaps in animals it is generally so postponed. Of mosaicism in animals we know very little. In the animal examples which are clearest the mixture is in respect of sex-characters, and we may be well content to see, with Morgan, in such examples a suggestion that some sex-chromosome or one of its constituents may be there mosaically distributed in the somatic tissues. Apart from sex-mosaics, the phenomenon so common among plants[1] is singularly rare in zoological material—a contrast which in any consideration of the difference between plants and animals should be remembered. Nevertheless in one remarkable example of frequent mosaicism, the intergrades between the "species" of *Colaptes*[2], where certainly the mosaicism is not a matter of sex, the multifarious distinctions can only by a severe strain on the imagination be attributed to the abnormal distribution of a single chromosome. As to the genetics of mosaic animals experimental evidence scarcely exists, nor have we any material likely to supply it. If the broken colours characteristic of so many breeds of animals were to be found on plants we might with great confidence expect them to be an indication of mosaicism and to be genetically unstable, but the geometrical relation of the animal to its germ cells is not like that of a plant. Perhaps the colours of Great Danes and of some Collie breeds, in which heterochromic eyes are common, may be mosaic in the genetic sense, but that is by no means certain. All we can see is that though a mosaic distribution of the factorial elements in the somatic tissues of a plant may and often must be an actual plan of the distribution of the several types of germ cells, no

[1] The great collection of records relating to bud-sports of all kinds is that of Cramer, P. J. S., "Kritische Übersicht der bekannten Fälle von Knospenvariation," *Natuurk. Verh. Holl. Maatsch. d. Wetensch.*, 3e Verzameling, Deel VI, 3e Stuk, Haarlem, 1907. Those who have no horticultural experience, who refer to Cramer's work, will appreciate what a conspicuous and frequent part somatic segregation plays among garden plants, attributable without doubt to their heterozygous nature. Incidentally Cramer gives many examples of distinctions in alleged root-cuttings, but in many of these, especially those so commonly witnessed in the propagation of Chrysanthemums, we must not in the absence of anatomical examination assume that the sources of the new shoots were structurally roots.

That the great majority of illustrations relate to colour-variation is presumably attributable to the facility with which colour changes attract attention. Structural changes of the same class are no great rarities. For striking recent examples see I. Andersson's work on *Barbarea* (*Journ. Gen.* XIV, 1924).

[2] See *Problems of Genetics*, p. 150, 1913.

such relation between germ cells and soma can exist in any simple animal in which the germ tract is early set apart.

We are reminded of mosaicism by the curious results obtained by Bagg[1] and Little in producing, by X-rays, an injury to the germ cells of mice, such that microphthalmus resulted in one or *occasionally* in both eyes, behaving as a recessive character. Later it was also discovered that a defect of the kidney was commonly associated with this lesion. We may have here something analogous to the condition of the germ cells in, for example, the variegated *Tropæolum*, which breeds true even though the somatic feature is a patchwork, and in segregation the "pure" is not reconstituted. Though exceptional in plants, this behaviour appears to be the rule among animals. The white Rosecomb Bantam, though always in our experience having a small coloured area, usually only two or three feathers, or even mere patches of colour on a few feathers, throws neither coloured nor white birds. The patch of colour is a definite constituent of the zygote which, on complete unpacking of the contents, comes to the surface. That this should be a normal genetical behaviour for a mosaic animal, though exceptional and somewhat unaccountable in a mosaic plant, is what the difference in the geometrical organisation of the two types of life leads us to expect.

The quantitative system of factorial analysis thus provides an adequate picture of the genetical behaviour of mosaic plants, in so far as it represents the properties of the two components after segregation, but the mode of that segregation still remains obscure. It might be conjectured that the mosaic cell has a mixed set of chromosomes which sort themselves out at random and thus reconstitute the two components pure, but this suggestion leads to difficulty as we shall immediately see.

Somehow a somatic cell is evidently able to divide in such a way as to produce cells dissimilar either from the parent cell or from each other, or both. The dissimilarity may be in the visible properties, as in differentiated tissues, or in such properties *and* in genetical potentiality also, as in the mosaics. In the progress of normal development we are familiar with divisions to which, so far as visible properties are concerned, the same description applies, and it is one of the paradoxes of cytology that, whatever the resulting tissue, its chromosome-content is the same, or at least shows no perceptible consistent distinctions; and—a phenomenon still more unaccountable

[1] Bagg, H. J., *Proc. Soc. Exp. Biol. Med.* XXI, 1923–4, pp. 146 and 228.

—though, as I understand, visible distinctions between the chromosome-contents are not uncommon in somatic tissues, yet they are not specially associated with visible mosaicism. If we conceive the progressive differentiation by which the petal of a Carnation, for example, is developed we must admit that, by a series of cell-divisions, colourless epidermal cells and coloured epidermal cells are both produced by division from a common origin, whether the resulting flower is bizarre or a picotee, and yet arguing from genetical properties we should have to believe that the distinction to which colour must be due is in the one plant a consequence of cytological difference and in the other plant that it is not. The dilemma is obvious.

Let us look at the alternative interpretation. The substances *seem* to be identical in the two plants. I should take this appearance as provisionally a reliable guide. The perceptible distinction between the mosaic bizarre and the differentiated colour of the picotee is one of configuration. Following that clue I anticipate that the solution is to be found not in any search for a distinction between the materials but in an analysis of the forces distributing them. In so far as a character is mosaically distributed in these plants, the very material, which might be treated as distributable according to the geometrical plan of normal differentiation, has escaped from that control. Whichever be the true account, the solution is to be sought in a proper understanding of the nature of the distinction between differentiation and genetical variation.

Cytology is providing some knowledge, however scanty, of the material composition of the cell, hut of the nature of the control by which a series of orderly differentiations is governed we have no suggestion.

At which of the somatic divisions a segregation can happen such as to produce mosaicism or a genetical distinction is quite uncertain, but the evidence shows conclusively that this phenomenon sometimes occurs, and that though it may be a sporadic event, it may on occasion exhibit features indicative of regularity.

In conclusion we do well to remember that in a few curious examples fertility is not attained until some special somatic segregation has taken place. Of these the Zonal Pelargonium, "Freak of Nature," is the most definite and remarkable[1]. The plant has both stems and the *centres* of the leaves of a peculiar white which may eventually become irrorated with green. The margins of the leaves, however, are solid

[1] See Chittenden, R. J., *Journ. Gen.* XVI, 1925, p. 48.

green, and being too large to fit the white centres they are thrown up into folds. In this condition the plant flowers but has abortive pollen which, though it goes through a reduction-division, is so defective that the small anthers shrivel away without bursting. The female side is also sterile. But when by some somatic division either component separates from the rest, forming a green stem or a white one, these on flowering are functionally fertile.

Having in view the various facts and considerations here enumerated I think we shall do genetical science no disservice if we postpone acceptance of the chromosome theory in its many extensions and implications. Let us distinguish fact from hypothesis. It has been proved that, especially in animals, certain transferable characters have a direct association with particular chromosomes. Though made in a restricted field this is a very extraordinary and most encouraging advance. Nevertheless the hope that it may be safely extended into a comprehensive theory of heredity seems to me ill-founded, and I can scarcely suppose that on a wide survey of genetical facts, especially those so commonly witnessed among plants, such an expectation would be entertained. For phenomena to which the simple chromosome theory is inapplicable, save by the invocation of a train of subordinate hypotheses, have been there met with continually, as even our brief experience of some fifteen years has abundantly demonstrated. Through all this work, with ever increasing certainty, the conviction has grown that the problem of heredity and variation is intimately connected with that of somatic differentiation, and that in an analysis of the interrelations of these two manifestations of cellular diversity lies the best prospect of success. Pending that analysis, the chromosome theory, though providing much that is certainly true and of immense value, has fallen short of the essential discovery.

A TEXT-BOOK OF GENETICS[1]

[*Nature*, LXXIV, 1906]

As the moment is favourable, may it be suggested that tbe branch of science the rapid growth of which forms the occasion of Prof. Lotsy's book should now receive a distinctive name? Studies in "Experimental Evolution" or in the "Theory of Descent," strike a wrong note; for, theory apart, the pbysiology of heredity and variation is a definite branch of science, and if we knew nothing of evolution that science would still exist. To avoid further periphrasis, then, let us say genetics.

Prof. Lotsy's lectures are a welcome contribution to genetics. They are expository and critical rather than creative, but there is plenty of room for such a work. Since it must be admitted that to most of us facts appeal "first when we see them painted," such a presentation as this book provides should attract many who would find little to detain them in original records.

There are twenty lectures in this first part, and a second part is promised. After a philosophical introduction, which must be left to the judgment of those versed in such matters, the author proceeds to a careful discussion of the evidence for direct adaptation. Though no Lamarckian in the usual sense, he has a high respect for Lamarck's penetration and breadth of view. In this revindication of a great name, naturalists of the younger generation who have studied Lamarck's writings at first hand will probably sympathise with Prof. Lotsy. In a limited sense the modification produced by environment —biaiometamorphosis, as Prof. Lotsy calls it—is important. No botanist doubts that the forms of plants can be profoundly changed by the conditions to which they are exposed. The normal or habitual form in which we know a species is only one of these modifications. Consequently each experimental proof of the dependence of form on environment has a direct bearing on the genesis of type. But the question of *purposeful* or adaptative modification is quite distinct, and of any transmission of purposeful modification in descent there is no evidence.

The section of the book which gives it its chief value is that in which an account is provided of the new developments in genetics, especially Mendelian analysis and the experiments of de Vries. The

[1] Review of J. P. Lotsy's *Vorlesungen über Descendenz-theorien*, 1 Theil, Jena, 1906.

consequences of Mendelian segregation are described with great clearness, and are illustrated by some excellent diagrams, of which one (p. 101) is striking and novel. The members of the various generations are shown in a perspective view, drawn approximately to scale, in a way which should do something to remove the supposed obscurity of these phenomena. Both the description of the facts and the critical discussion of the bearing of Mendel's discovery on the earlier or Galtonian method of calculating inheritance are especially lucid and to the point.

The weaker features of this section are such as are almost inevitable in attempts to confine a rapidly growing study within text-book limits. The relative importance of the various elements is continually changing. For example, though due stress is laid on Tschermak's fine series of cases illustrating the influence of hidden factors, or cryptomeres, Cuénot's useful exposition of the part played by double factors in the case of mice seems to have been left out. Having regard to the remarkable developments which have followed, this omission is unlucky. In the same connection it is a matter of special regret to myself that the revised and simplified account of the "walnut" combs in fowls did not reach Prof. Lotsy in time to prevent a reproduction of my former and erroneous idea in his text-book.

By all who are working at genetics the discussion of de Vries' mutations will be read with interest. Till now those remarkable observations have been regarded either with indiscriminate enthusiasm, or with still more unreasoning suspicion. But on those who know that the mutations of Œnothera are not errors of observation, and hesitate to accept them as the single key to the final mysteries of evolution, the question begins to press: What *are* those mutations? Upon this point the teaching of genetic research is clear. Before we can form a definite view as to the nature of any given mutation we must know its gametic relations to the type from which it sprang, and to the sister-mutations. So far, these relations, as expressed by the ratios in which the forms appear, seem to be almost always irregular in the Œnothera cases. Experience, however, has shown that such irregularities, as in the case of Miss Saunders' *Matthiola*, may conceal an underlying regularity which fuller analysis can reveal. For instance, we know that various individuals of a form A may give respectively an F_2 ratio $9A : 7B$; or $3A : 1B$; or all A; or $27A$, $9C$, $28B$, and so on, and the causation or meaning of these several ratios is clear. May not such complexities be the source of the confusion which apparently besets

the Œnothera cases? That is the opinion to which Prof. Lotsy inclines, and the position is for the most part unassailable as yet. All that can be positively asserted is that these mutations are forms arising discontinuously, and that their distinctions are exactly comparable with those that often appear to characterise species. But now that we understand what a medley of phenomena is included in the term "specific difference" it becomes necessary to go further and to ascertain which phenomenon is exemplified in each case. That genetic analysis can alone answer that question everyone now perceives. De Vries' own discussion of his results contains manifest traces of an attempt to incorporate the Mendelian ideas into earlier and pre-Mendelian conceptions, and the result is not always harmonious or convincing. We look to de Vries and the many observers who are now at work on Œnothera to bring the various possibilities to a strict test, case by case, and so complete what has been begun with such astonishing success.

Meanwhile, however, it must be conceded that there are serious difficulties in the way of a purely Mendelian account of the Œnotheras —more perhaps than Prof. Lotsy indicates. Of these one of the most formidable is the behaviour of the form *nanella*, for which other cases afford no parallel. There are, further, the objections de Vries himself has urged in the passages contributed to Moll's exposition of his work —particularly, that no indication of a hybrid origin of his original stock is forthcoming. Again, though the sterile pollen grains are suspicious, I may mention that in a collection of wild Œnotheras (? species) made near Baltimore, I found none which had not some bad pollen grains. Were all these hybrids? it may well be asked. If so, hybrids of what? Our Rubi hybridise freely, but, as Focke showed, there are pure forms with perfect pollen, and hybrid forms with an admixture of bad grains. This test should be made in America on a large scale, to discover whether any Œnothera is "pure" by that criterion.

But again, we know that the production of analytical varieties by a hybrid, and the production of novel forms by a mutating species, must be exceedingly similar and perhaps indistinguishable phenomena. Hybridisation cannot be regarded as the sole source of analytical variation—witness the case of *Primula sinensis* and the sweet pea, where analytical variation is rife, though no hybridisation has taken place. The interrelationship of the two sets of occurrences is still obscure; but by experimental breeding it can in great measure be

elucidated, and in the course of that inquiry the meaning of mutation will probably be discovered.

Only salient features of the book have been mentioned; many others must be passed over. *Capsella* has provided (p. 180), as might be expected, good examples of the constancy of *petites espèces*. Time brings revenges, and we must hope that Jordan would have felt satisfaction in the recognition now accorded to his once discredited work, though, by the perversity of things, that work is used to complete and support those views he most detested. Strange, too, would it seem to his opponents to see Jordan's microspecies received as a valuable element in the general doctrine of mutability!

In several minor points the book is open to criticism. The Artemia-Branchipus story should not be repeated even incidentally without words of caution. The pictures even in these half-tone days are below the mark, and such pictures as those of peloric Linaria make one long for decent woodcuts again. The figure of the Norwich canary would surprise the fanciers of that city, and it suggests that the crest is a Norwich character. Lastly there is a profusion of most distracting misprints.

LECTURES ON EVOLUTION[1]

[*Nature*, LXXVIII, 1908]

THE second part of Prof. Lotsy's book contains the substance of twenty-eight lectures, completing his course on evolution. Though making no claim to have broken new ground, the work is of real use. The presentation of contemporary knowledge of these subjects which it gives is comprehensive in scope and accurate in treatment. The author does not suffer from the delusion that in evolutionary science finality was reached fifty years ago, and it is a pleasure to see the results of modern research incorporated without ludicrous mistakes. This is probably the best text-book of the subject yet compiled.

There are occasional signs of vacillation between the old and the new conceptions. For example, as an instance of a dissimilarity between reciprocal crosses, Prof. Lotsy brings forward *Bilbergia nutans* × *vittata* on evidence which would have satisfied the older observers. Knowing the sources of ambiguity which affect such evidence, he remarks that possibly the dissimilarity may nevertheless be due merely to "Pleiotypie in F_1." Rather, until it shall have been ascertained by repeated experiment that there is consistent dissimilarity between the reciprocals, the presumption is strong that the differences observed are an expression of heterogeneity in the cross-bred generation as such, and are not dependent on the parental *rôles* allotted to the respective species. The break with tradition which Mendelian discovery has made is, indeed, so wide that a generation must pass before the older interpretations disappear, and evolutionists come to think easily and habitually in terms of the new system. This book will do a good deal towards accelerating the change.

To professed students of genetics this text-book may be recommended as bringing a quantity of fresh materials under consideration which have not previously been dealt with in a consecutive treatise. Of these materials some are ancient and some modern. For the first time, probably, Gärtner's work is presented in summary, and though, judged by modern standards, his experiments are fragmentary and imperfect, many readers will thus become aware of the range of observation which they covered. In another useful chapter a clear abstract of Nägeli's views is provided. Prominence is given to the remarkable experiments of Klebs on *Sempervivum Funkii* showing

[1] Review of J. P. Lotsy's *Vorlesungen über Descendenz-theorien*, 2 Theil, Jena, 1908

the influence of external conditions. Facts of this class are extraordinarily difficult to interpret, and until exhaustive work has been done on the same lines we must perhaps abstain from confident interpretation altogether. As a subject for genetic research the Sempervivums are most attractive. To turn over Jordan's plates of this polymorphic genus in the "Conspectus"—still more to see his actual collection of living plants now preserved in Miss Willmott's garden—is to realise the great possibilities which the material provides. It is to be hoped that someone will devote himself in good earnest to an analysis of these protean forms.

The book suffers from want of compression, and there are some repetitions. The long chapters on the geographical aspects of the problem serve rather to show how little help must be expected from that line of inquiry until much more minute treatment can be applied. No one supposes that any fresh lesson of importance is to be derived from the broad facts of geographical distribution, and the deductions that have been already drawn could, in so far as they are of consequence, be amply stated in half a dozen pages. On the other hand, as to the more interesting phenomena of geographical interrelationship, the problems, for instance of intergrading species, too little is said. In a text-book of this scope it would have been well to direct the attention of students to the necessity for thorough study of facts of this class, a field in which there is room for much analytical research.

There is one rather serious omission. The phenomena of regeneration and the mechanics of development are among the most obscure with which a theory of descent has to cope. In the minds of many evolutionists, the existence of those strange and specific powers of response to injury which modern research has revealed, constitutes a formidable problem, and though for its solution we still wait, the facts should have been stated.

In dealing with matters of opinion, Prof. Lotsy shows good judgment and critical power. This is especially manifested in his discussion of adaptation, of the evidence for mutation, and of the assertions by which an attempt has been made to revive Lamarckian views. Sometimes, perhaps one is conscious of an exaggerated patience. Conventional arguments which the anthor plainly recognises as bad are repeated out of deference to their originators. The expert is not in doubt as to his real opinion, but the lay reader will carry away the impression that decided questions are still open. When he deals with

the writings of Wallace, indeed, he allows himself the remark that *this is "Selectionstheorie à outrance," but such freedom of expression* is rare.

The author gives a full but somewhat non-committal account of the views of Eimer, and discusses the relation of Nägeli to the conception of orthogenesis as a main factor in evolution. Yet, after reading all that is said on this question, it is not easy to seize the exact point which is relied on as a proof of the reality of orthogenesis. The adaptation may be very perfect, and selection of indeterminate variations an unpromising account of the origin of that perfection, but it will never do to attribute this wonderful power of orthogenetic variation to organisms simply because we do not see how they could have become what they are without it. This, apparently, is Prof. Lotsy's view also, but many would have been glad of a more definite lead.

If the book reaches a second edition, as it probably will, the question of reducing it to two-thirds its present size should be considered. In that event also the proofs should be submitted to a professional proof-reader, for in this second part, as in the first, the abundance of typographical slips exceeds all reasonable limits.

RECENT ADVANCES IN THE GENETICS OF PLANTS[1]

[*Nature*, LXXXVIII, 1911]

PROF. ERWIN BAUR is well known to students of genetics as a most successful investigator. The fifteen lectures included in the present volume were delivered as a course in Berlin, and they constitute an admirable text-book of the subject, which will do much to familiarise Continental biologists with the methods of Mendelian analysis and the deductions to which it has led. The coloured pictures are exceptionally good. No clearer or better illustrated account of the present state of knowledge of these matters could be desired.

Some years ago Prof. Baur began a series of researches into the nature of variegation in plants, without any special intention of investigating Mendelian phenomena, but, like so many others engaged on special problems, he soon found that a knowledge of heredity was indispensable to a proper understanding of his subject. The breeding experiments then instituted, though begun as a side-issue, have illuminated the whole field. His first success was obtained in a study of the golden-leaved Antirrhinum, which he proved to be a heterozygous form, possessing only one factor for greenness. Self-fertilised, it gives two yellows to one green, the missing term in the series being the homozygous albinos which perish on germination.

This led to a comprehensive examination of the inheritance of flower-colour in *A. majus*, a subject also studied by Miss Wheldale in this country. The series of types is very large, seeming at first sight almost continuous, and the analysis was exceptionally troublesome, but it is satisfactory to know that though working independently, both observers have arrived at practically the same conclusions as to the factorial composition of the several forms. In this book Antirrhinum is naturally taken as the typical example of the effects of combinations of long series of factors, and the reader who masters this example will have encountered most of the complications which ordinary Mendelian inheritance presents.

From this work on the varieties of a single species Baur has gone on to less familiar ground, and in this book he gives the first results of his experiments on the interrelation of forms which are quite distinct species in the systematic sense, especially *A. majus* and *A. molle*. The F_1 plants are fully fertile, and F_2 shows a long series of diverse types

[1] Review of E. Baur's *Einführung in die experimentelle Vererbungslehre*, Berlin, 1911.

resulting from the recombination of segregating factors, but the analysis is still to be completed. One observation of extraordinary interest is announced, namely, that the self-sterility of *A. molle* is a recessive. This announcement must be regarded as preliminary, but if established, the discovery will constitute a striking advance. Self-sterility is one of the greatest paradoxes in nature. If it is true, as we are almost forced to believe, that a self-sterile plant can be fertilised by the pollen of *any* other individual but not by its own, then each individual is differentiated by virtue of its individuality, and there are as many classes as individuals. The notion once suggested by de Vries, which I also had formerly entertained, that there are in reality several *classes of individuals and that probably fertilisation was inoperative* only within each class, is negatived by such experiments as have been made by others and by myself (on a small scale in *Linaria vulgaris*). If self-fertility be a dominant, the main mystery is still unsolved, but we have a new fact of great consequence which may lead to a solution.

The most important chapters are those in which Baur describes his discoveries regarding the inheritance of the several forms of "Chimæra," the term Winkler has introduced to denote patchwork or mosaic individuals. In a variegated Pelargonium, for instance, the albino parts of the vegetative organs may be *sectorial* forming radiating patches of white, or *periclinal*, in which case the external layers of cells may be green and the internal white; or conversely the internal may be green and the external cells white. Baur has shown that the colour of the offspring, whether green or white, depends on the nature of the sub-epidermal layer of cells from which the parental germ cells were derived. If in the periclinal chimæra the two peripheral layers of cells are green, the offspring (of self-fertilisation) are all green; if the peripheral layers are albino the offspring are all albino, and, of course, perish. If only the outer cell-layer is white the offspring are green. In either case the particoloured character does not reappear in the offspring. From the sectorial chimæras the inheritance is more complex, and much remains to be cleared up. This discovery of the significance of the sub-epidermal layer is one of very great importance, and we may anticipate that it will lead to remarkable extensions. It may not improbably lead to a reconsideration of the generally accepted doctrine that segregation takes place in gametogenesis.

Baur has applied these observations to the interpretation of the curious "graft-hybrids" between *Solanum nigrum* and the tomato, first made by Winkler. Some of these were obviously sectorial patch-

works of the two species, but Baur suggested that of the others some were actual periclinal chimæras, in which a foundation of tomato was enclosed in one or in two cell-layers of *S. nigrum*, or conversely *S. nigrum* enclosed in an outer sheath of tomato tissue. This conclusion was at first strongly resisted by Winkler, but in a preliminary communication he has since announced the proof that it is correct, having himself by cytological investigation of the growing points of the periclinal forms been able to prove that some of the layers have the chromosome numbers proper to *S. nigrum*, and others those of *Lycopersicum*. We can scarcely doubt that this remarkable series of observations will pass into the classics of biology.

On similar lines Baur proposes to elucidate the old problem of *Cytisus Adami* and *Cratægo-Mespilus*, the two traditional examples of "graft-hybrids." The former, for instance, is regarded as a Laburnum enclosed in a sheath of *C. purpureus*. On occasion, as when the exterior is wounded, the Laburnum can come out and develop. Baur's idea is doubtless a part of the truth, but I cannot clearly apply it to all the phenomena which *Adami* presents, especially to the sexual vagaries which it shows in this country at least. In it the *Adami* flowers have good pollen but no good ovules; the *purpureus* flowers have the female parts developed, but the anthers bad; while the *Laburnum* flowers are perfect and set seed in plenty. Nor do I clearly understand the origin of the *purpureus* branches. One can scarcely help suspecting that in the segregation by which these phenomena are produced there is some complex repulsion between the sex-factors and the factors for colour or form, comparable with the distinctions now known to exist between the genetic constitution of pollen and ovules of the same individual in several cases, *e.g.* Stocks and Petunia (Miss Saunders), or Œnothera (de Vries).

The only point in this excellent book which calls for criticism is, in my judgment, the rather crude representation of segregation as effected by chromosomes. These pictures will live in the memory of the reader, and tend to limit his imagination of the possibilities more closely than the known facts at present warrant.

THE MECHANISM OF MENDELIAN HEREDITY[1]

[*Science*, N.S. XLIV, 1916]

STUDENTS of genetics some six years ago learned with lively interest that Professor Morgan had discovered in the fly *Drosophila ampelophila* an example of inheritance parallel to that seen in the well-known descent of colour-blindness in man. Substituting red eye and white eye in the fly for normal colour-vision and colour-blindness respectively in man the phenomena were exactly similar. Hitherto no such case in an animal available for experiment had been known. We were aware of several instances, notably that of the moth, *Abraxas grossulariata*, the pigmentation of the silky fowl, and certain others in poultry, canaries and pigeons, in which analogous descents had been traced; but in all these the parts played by the sexes were reversed. From this evidence indeed it had been proved that in the moth and the birds the unfertilised *eggs* are differentiated into two classes, those destined to become females and those destined to become males. Obviously enough it would be inferred from the descent of colour-blindness that in man the *sperm* was similarly thus differentiated into two such classes, destined to form females and males respectively, a phenomenon which Wilson and others had cytologically demonstrated in various insects. At this point the matter rested.

With the discovery of the peculiarities of *Drosophila* genetic research has passed into a new phase. The animal breeds rapidly, going through many generations in a year. It is inexpensive to breed, and the families consist of numbers which, relatively to those attainable in most subjects, are enormous. Since it first attracted Professor Morgan's attention it has been found to produce a long and intricate series of factorial varieties, or "mutations" as the authors prefer to call them, differing in the colour of eyes and body, the sizes and shapes of the wings, and other respects, the number of these differences being now computed at more than a hundred. Professor Morgan and a band of enthusiastic colleagues set themselves with the utmost zeal to analyse the interrelations of this mass of factors. Half a million flies have been bred, with the result that the data respecting the genetics of *Drosophila* in quantity now surpass those obtained from any other animal or plant. The advances made are on any

[1] Review of *The Mechanism of Mendelian Heredity* by T. H. Morgan, A. H. Sturtevant, H. J. Muller and C. B. Bridges: New York, 1915.

estimate many and of quite exceptional significance. That much is certain. If we go further, and accept the whole scheme of interpretation without reserve we are provided with a complete theory of heredity, so far as proximate phenomena are concerned.

We may perhaps best approach the subject by reference to a class of facts witb which all investigators are now familiar. Of the factorial differences detected in *Drosophila*, many of the more important were soon shown to be sex limited, as we used to call it, the "limitation" being to males, just as in colour-blindness and some other sex-limited affections in man. From an analysis of the descents of these characters Morgan concludes that such limitation is in reality only a special case of that complete or partial association of factors in their parental combinations which was first recognised as coupling and repulsion. These phenomena may in fact be all one. They are examples of inkage between factors, the second factor involved in the case of ex limitation being that for sex. The fundamental identity of these inkage phenomena had naturally been suspected. Difficulty, however, lay in the peculiarity of sex limitation, that in it the linkage has never been observed to be other than complete. The new theory, as will be seen, represents this distinction in a simple and readily coneivable way, so that we are at once attracted. It may be remarked hat linkage is no mere incident of technical genetics. We can readily erceive that it must play a great part in the control of heredity. lose resemblances of offspring to parents and grandparents in eatures and other attributes are common even in families of mixed aces like our own. Such resemblances must depend on the coxistence of multitudes of factors, and could scarcely ever be perceptible if the factors were really distributed at random among the erm cells. The theory provides a mechanism by which their associaons may be governed.

From the beginning it was tempting to interpret the processes itnessed in the maturation of the germ cells as the visible means by hich factors are segregated. Cytologists have shown that when the romosomes are formed anew from the rested nucleus their number d on the whole their forms are constant for the species. They may us be regarded as having a permanence or individuality. Further, ey consist of pairs, one of each pair doubtless representing the aterial contributed by each parent, tbe two contributions having ained their identity through all the divisions and changes which ve happened since the original fertilisation.

If, therefore, the number of genetic factors were never greater than the gametic or haploid number of chromosomes, we should obviously *conclude that each chromosome carried one factor*, and the ordinary distribution of factors would be produced by a random allocation of one chromosome from each pair to the set comprised in each gamete. But we know that the number of genetic factors in various types of life greatly exceeds the gametic number of chromosomes and consequently this simple account was discarded as insufficient. At this point we meet the first of the far-reaching suggestions which[1] Morgan offers, *namely that all the factors are linked together in groups, and* that the number of the independent groups is that of the haploid chromosomes. This number in *Drosophila* is four, and it is claimed that, on genetic analysis, the various factors of *Drosophila* can be proved to be so interrelated as to constitute four linked groups and no more. Before wholly accepting a proposition of such magnitude we naturally entertain a provisional reserve, but it may be at once admitted that all the evidence available is capable of this construction. Among the animals and plants already studied are many in which the factors, apparently subject to no linkage, in number far exceed that of the haploid chromosomes, but Morgan is able to reply with force that the possibility of linkage in these cases has not been exhaustively investigated. Tests of the heterozygotes by breeding with double recessives on a considerable scale provide the only really sufficient method of detecting linkages. Such work (especially in plants) is commonly very laborious and has rarely been carried out. Thus, though the presumption would *à priori* seem to be rather against the view that linkage will be found so abundantly operating even in the familiar examples, the speculation is quite legitimate. That it is extraordinarily promising as offering at least a chance of positive progress must be obvious to all.

But if the factors enter the offspring in linked groups—the chromosomes of each pair representing severally the parental combinations—the formation of new combinations inside any one group must mean that there has been an interchange or "crossing-over" between the two homologous chromosomes. We know that such new combinations can be formed. Gametes bearing them are produced in all cases in which the coupling or the repulsion—to use the older terms—is not complete. To account for the crossing-over of factors from one chromosome to its mate Morgan appeals to certain phenomena of twisting and interlacing of chromosomes in synapsis, first made

prominent by Janssens, who observed them in Amphibia. It is suggested that in the course of this process of twisting the chromosomes may anastomose and again break, exchanging parts of their substance. For those unversed in practical cytology it is not quite easy to judge how far this hypothesis is in accord with observed fact. That twisting takes place in many types, especially Amphibia, is clear; but neither the figures reproduced from Janssens nor the originals from which they are taken—still less the very fragmentary observations of both Stevens and Metz from *Drosophila*—provide more than a slender support for this most critical step in the argument. It is to be hoped that the authors will before long tell us exactly upon what evidence they are here relying.

The formation, then, inside a linked group, of factorial combinations other than those which entered from the parents, is ascribed to crossing-over from one chromosome to its fellow or mate. At an early stage in the work, the curious and very significant fact was observed that in the male no such crossing-over took place in regard to the various factors which had been proved to be *sex-linked*. The cytological interpretation of this discovery was ready to hand. In many forms, especially insects, the sperms have been proved to be of two kinds, those possessing an *X*-chromosome, destined to form females, and those without this chromosome, destined to form males. If therefore the *X*-chromosome carried the sex-linked factors—a supposition inevitable inasmuch as these factors are all destined to go into the daughters—and if there is no real mate to the *X*-chromosome, evidently there can be no interchange or crossing-over here. Therefore in the case of sex-limited characters linkage is complete.

On tracing the growth of the theory or group of theories which have been built up on the *Drosophila* evidence the consideration just propounded stands out as the original foundation stone. It was so introduced in the chief inaugural paper of the series. This "sex chromosome in the male has no mate," Morgan tells us, and consequently no interchange with it takes place[1].

On reference, however, to the work of Miss Stevens (1908) whose paper is given as authority for the mateless condition of the *X*-chromosome in *Drosophila ampelophila*, we read that she found extreme difficulty in studying the cytology of this creature, but ultimately satisfied herself that there is an unequal pair. The more

[1] *Journ. Exp. Zool.* XI, 1911, p. 383.

recent cytological work of Metz relates entirely to the female, but in a note on the male he remarks

so far as my observations go, they indicate an unequal *XY* pair in the male, without any additional piece attached to either. Neither my observations nor those of Miss Stevens are conclusive, however, owing to the difficulty of observing the chromosomes in these stages. The question is important *for the bearing it has upon the breeding experiments with this fly, and we* are doubly unfortunate in being thus far unable to settle it[1].

In 1913, Sturtevant in introducing the first formal development of the theory of linear arrangement, presently to be considered, repeats that there is no crossing-over among the sex-linked group of factors in the male, "since the male has only one sex-chromosome[2]." When we come to the book of 1915 the same authors have an entirely different conception of the cytological phenomena. There are two sex-chromosomes in the male, and though as a matter of convention, one of them is represented as different from the other in shape, the reader is very properly told that the distinction has not yet been observed[3].

Without insisting too much on the point, we cannot avoid noticing that this complex web of theory is so exceedingly elastic as to be capable of being fitted to a framework of cytological fact, the converse of that for which it was designed. Still, as some animals are found to have no second heterochromosome the suggestion that such a body, when present, may be inoperative might be offered in extenuation.

Presently we meet, however, a fact which is much more difficult to harmonise with the theory, though constituting one of the most novel and remarkable of the discoveries made in the *Drosophila* work. Not only do the sex-linked factors show no crossing-over in the male, but experimental breeding shows that in the male there is no crossing-over even of the factors composing the other groups. *Crossing-over, in fact in* Drosophila, *turns out to be exclusively a phenomenon of the germ cells of females.* This is a genetic discovery of the first magnitude, whatever its ultimate significance, but the cytological interpretation of crossing-over must now bear a very considerable strain: for, on the one hand, though the absence of crossing-over in the sex-linked characters had fitted well with the

[1] *Journ. Exp. Zool.* XVII, 1914, p. 49, *note*.

[2] Sturtevant, *ibid.* 1913, p. 44.

[3] In the recent paper of Bridges (*Genetics*, I, 1916) the distinction in shape is stated to be a reality.

belief that the sex-chromosome in the male was unpaired, this chromosome is now admitted to be paired; and on the other hand the characters ascribed to the chromosomes known to be paired turn out to be equally unable to cross-over in the male. It is with some surprise that we find neither in the book nor in the material previously published any coherent discussion of the difficulties thus created. If further cytological work shows that the chromosomes of the female twist and anastomose, but that those of the male do not, the chromosomal theories of heredity will receive a very remarkable support. Meanwhile on this part of the subject there is little more to be said.

Recombination then within the limits of a linked group is regarded as a consequence of crossing-over, or the interchange of parts between one chromosome and its mate or homologue. This conception, whether well or ill founded, has led on to a further and very remarkable speculation. If the factors are carried by the material of the chromosomes, what more likely than that they, or rather the particles severally bearing them, should be arranged in a row, like a string of beads, along the length of the chromosome? The proportion of cross-over gametes might thus give an indication of the actual relative positions of the factors along the chromosome. On this inspiration, the intertwining of two strings of beads providing always the mechanical analogy, the numbers in the experimental families have been carefully studied. The percentage of cross-overs is taken to indicate the position of the factors. Where there is no linkage, this percentage is, of course, 50, all combinations occurring in equal numbers. But if two factors *AB* show 50 per cent. crossing-over and both *A* and *B* can severally be proved to be coupled to a third factor *C*, then all three may in reality be members of one linked group, and the fact that in the case of one pair there is 50 per cent. of crossing-over may be a consequence of the relative positions of these factors in a linear series. The amount of crossing-over can thus be interpreted as an indication of the relative position of each factor in such a series. Upon this follows the great thesis of the book: that this series is in fact a row of points along each of the four chromosomes, and that the redistributions or recombinations of characters can be correctly represented by strings of beads which twist together in pairs, breaking and joining each other at nodes. Whether this conception is sound or not, we accept it as a gallant attempt to move on. No other of equal promise has been offered and we must observe its development with cordiality and respect.

Confronted with a theory of so much novelty and importance, the reader's first desire is to examine the details of the evidence from which it has been deduced. A serious charge lies against the book inasmuch as the material for such an examination is not contained in it. We are provided with a sketch—a vigorous and impressionist sketch—of the facts as the authors see them, but we want a much nearer view. Pending this, judgment must be suspended. We are told that the breeding numbers prove the factors to be in four linked groups. We would like to take each one separately and follow the proof regarding its linkages. As yet there is no means of doing this. Of the evidence the book avowedly gives illustrative specimens merely, and even the long array of *Drosophila* papers leaves great gaps unfilled. Take the first or sex-linked series. The book tells us that more than 40 factors have been located in it and arranged in order. Respecting the great majority we have no details at all and as to most of the remainder very few. There are, however, six that we can examine in the light of the data summarised by Sturtevant in *Zeits. f. Vererbungsl.*, 1914, the last considerable body of evidence to hand.

The factors concerned, called *Y*, *W*, *V*, *M*, *R*, *Br*, are represented as arranged along the chromosome in such a way that two, *Y* and *W*, are at the zero end, two more, *V* and *M*, near together at 33·5 and 36·5, and the remaining two, *R* and *Br*, also near together at 53·3 and 57·7. The numbers indicate that the members of each set of two are closely linked, for with fair consistency the breeding ratios are those characteristic of close "coupling," namely, *nAB* : 1*Ab* : 1*aB* : *nab*, and of "repulsion" in the form 1*AB* : *nAb* : *naB* : 1*ab*, the value of *n* being much greater than 1. The relations of *Y* and *W* to *V* and *M* are also of this kind, the coupling being of course less close. But taking *Y* with *R*, *W* with *R*, *V* with *R*, or *M* with *R*, we meet numbers of a very different order, and it is not clear by what system they have been interpreted. For instance, we find the following extraordinary series given,

for *Y* with *R*				
as *repulsion*	342	58	466	19
as *coupling*	235	50	194	56
for *W* with *R*				
as *repulsion*	567	143	697	91
as *coupling*	294	61	175	108
for *V* with *R*				
as *repulsion*	147	147	520	36
for *M* with *R*				
as *repulsion*	430	795	1716	189
as *coupling*	4189	93	850	1033

The numbers in which the new combinations come are then added in each case and set out as percentages of the totals, these percentages being taken as indications of the linear distances between the loci in which the factors are presumed to be. To those accustomed to series of this class, these numbers are so aberrant as scarcely to suggest *primâ facie* that they represent Mendelian series at all, and it seems at least improbable that they can be used to calculate percentages comparable with those obtained from the various comparatively normal series by which for instance *Y* and *M*, *V* and *Br*[1], *Y* and *W*, or *W* and *M* are interrelated. Throughout the experiments indications of differential viability recur, largely masking the true proportions of the classes, but as has been remarked by the autbors in reference to certain special cases, the incidence of this differentiation is so irregular that allowance cannot be made for it in any consistent fashion. Meanwhile the data look so intractable that a doubt has sometimes arisen whether the account here given may not be a consequence of some radical misunderstanding of the author's meaning.

One is tempted further to ask whether all parts of the several proofs are really independent of each other. In the present state of the evidence only the authors themselves can positively answer this question. They declare that all the factors are proved to be disposed in four separate systems of linkage, but the argument that they are thus arranged contemplates a very great variety of possibilities not obviously included in this scheme. For example, the fact that two pairs of gens or factors give 50 per cent. of cross-overs might in the authors' view be a consequence of the location of the two pairs in distinct chromosomes. It may equally be a consequence of the two being in the same chromosome but at the terminal and central positions respectively. It may also be produced by double or triple crossing-over, and in other ways also. Moreover, granting that the factors seem to be related to each other in four systems of linkages, it must next be proved that there is no linkage between members of distinct systems. The evidence of such independence is admittedly meagre, and indeed as to the behaviour of the factors comprised in the third system we have been told very little at all.

[1] The numbers given for *V* and *Br* by Sturtevant are misprinted, 260 standing for 2660. Thus emended tbey are fairly normal. The worst examples all involve *R*, and it might be suspected that this was a source of special difficulty, but analogous numerical abnormalities occur also in the "second chromosome" series, nor can any hypothesis of differential viability be readily applied to such figures as those quoted above.

The machinery for dealing with unconformable cases is extraordinarily complete. Besides differential viability we hear of some twelve lethal factors by whose operation certain classes may be extinguished; changes in output with age; a special phenomenon spoken of as "interference" inside single chromosomes; some interaction between chromosomes; even of a factor modifying the normal amount of crossing-over, and lastly of an altogether distinct kind of crossing-over in the four-strand stage. Can the action of all these processes be severally traced? Can their consequences be distinguished from each other, and especially from those of multiple crossing-over? There remain, of course, also the various slips to which all experimental work is liable, such as in this case errors from the overlapping of generations—several times alluded to as a real danger—and others similar which no doubt have been obviated more or less with the improvement in technique. Apart from obscurities of this more superficial kind, is it clear that the series of alternative hypotheses is capable of ultimate analysis? As has been already said, the authors may be able to make such an analysis, but they have not yet offered it to the reader in irrefragable form. Meanwhile the suspicion is unavoidable that, given a conviction that the factors *must* be arranged in rows along four chromosomes, the various interpretations provide rather a method, or perhaps we should say alternative methods, by which the facts can be reconciled with the hypothesis, than a proof that this hypothesis is correct.

Ever since the discovery of systems of linkage it has not been in dispute that several factors, perhaps all, are arranged in some ordinal system or systems. We are dealing with phenomena of *lineage*. The hypothesis of reduplication was offered as one way in which the processes could be logically represented, at least in plants. It is admittedly a very crude conjecture, but it has the merit of being non-committal and applicable to units of various magnitudes. So much may be remarked in parenthesis; but the critical point now is whether in the various forms of life the number of independent factors, or systems of factors, is or is not greater than the haploid number of the chromosomes. The determination of this question all students of genetics will now await with keen interest.

In all the various parts of the subject explored, whether the main theory prove ultimately to be truth or fallacy, there can be no doubt as to the extraordinary value of the *Drosophila* work as a whole. Of the discovery that may perhaps come hereafter to be regarded as the

most illuminating of all—the phenomenon of "non-disjunction"—we have still to speak. The exploration of this group of facts has been made by Bridges, who, since the brief note contained in the book, has published in *Genetics* a detailed account of his experiments. With this publication it must be admitted we are lifted on to something like solid ground. Hitherto amidst all that cytology has contributed, in one respect only has it been found possible to connect quite positively cytological appearances with somatic characters. That in certain forms of life sex is connected with the X-chromosome is the one unambiguous fact.

To this Bridges now adds evidence of a new and very remarkable kind. In crosses between females with recessive eye colour and normal "wild" males, the daughters normally resemble the father and the sons the mother. As exceptions, "matroklinous" daughters are produced, that is to say in this case with eyes of the recessive colour. It was argued *à priori* that such a result might be reached if the *two* X-chromosomes of the female were by some chance together passed into an ovum and that ovum were fertilised by a Y-bearing sperm. Such a zygote would be female by virtue of the two X-chromosomes. But for this it would have been male, for it is fertilised by the sperm normally destined to males. Since also all the dominant sex-linked factors possessed by normal males are borne by the sperm normally destined to daughters, the sperm that the exceptional daughter receives is recessive, and therefore these daughters are matroklinous. It follows as a corollary from this argument that fertilisation might take place between ova bearing no X at all and a sperm bearing X, and it is said that such a class has been actually recognised as consisting of sterile males. Once the matroklinous daughter has appeared, by breeding from her, a complex variety of consequences may be expected, all deducible from the *à priori* analysis. In the breeding experiments, apart from certain numerical aberrations still unexplained, these have now all been realised experimentally.

Cytologically also the expected appearances have been found—in the sense that egg cells of the "exceptional" females have been seen to contain three instead of two of the chromosomes which the authors now agree are the heterochromosomes. Moreover, from an XXY female it should be possible to breed an XYY male and the two in combination may lead to forms with $XXYY$, and figures are given showing that these also have been produced and cytologically demon-

strated. No one can doubt that this is a very fine achievement. Though still sceptical as to the adequacy of the theory of cross-overs and especially of the soundness of the arguments by which the factors are assigned to serial positions in the chromosomes, it is difficult to see how we can deny that the sex-linked characters have some very special relation to the sex-chromosomes.

In our present ignorance of the nature of life we cannot distinguish cause and effect in these phenomena and it is not possible to attach any satisfactory meaning to the expression that the sex-linked factors are "carried" by a chromosome, but if any one wishes to describe the association of the phenomena in that way there is nothing to forbid him. The properties of living things are in some way attached to a material basis, perhaps in some special degree to nuclear chromatin; and yet it is inconceivable that particles of chromatin or of any other substance, however complex, can possess those powers which must be assigned to our factors or gens. The supposition that particles of chromatin, indistinguishable from each other and indeed almost homogeneous under any known test, can by their material nature confer all the properties of life surpasses the range of even the most convinced materialism. Hence it may well he imagined that even if cytologists decide that in synapsis there is no anastomosis and no transference of material, the effective transference of the gens may occur. The transference may be one of "charges." Perhaps even we might profitably consider whether the chromosomes may not be thrown up, and the gens grouped along their lines by the interplay of the same forces.

Though as must frankly be admitted the *Drosophila* work is on the whole favourable, and in certain respects strongly favourable, to the view that all segregation is effected at the reduction-division, it may be well to remind the workers in this field of the phenomena which are inconsistent with that conception. There are, of course, the old difficulties that if the chromosomes play this prerogative part we should expect some broad consistency between their differentiation and that of the forms of life, and we should not anticipate that they would be capable of great irregularities of number and behaviour. But apart from these there remain the perfectly authenticated instances not merely of somatic differentiation in regard to Mendelian characters, but the whole range of bud-sports and chimæras of various kinds, and lastly the indubitable evidence that the male and female sides of the same plant may have distinct genetic properties. Such

facts, to be sure, are no indication as to the powers of chromosomes, but they are a strong indication that the reduction process is not the only moment at which segregation may be effected. Presumably the advocates of chromosomal views would admit that these are exceptions, but still they are exceptions of a most significant kind. Conceivably we may be led to the conclusion that there is some radical distinction between plants and animals in these respects.

Many matters of importance are treated in the book, especially the vexed question of the nature of "mutations," to which no justice can be done here. All that can be now attempted is an outline of the essential discoveries. To some it may seem that the disposition of this article is towards undue scepticism. To doubt the theory of cross-overs, for instance, at this date is almost in effect to "draw an indictment against a nation," which we know on high authority is an impossible task. Let it then be explicitly said that not even the most sceptical of readers can go through the *Drosophila* work unmoved by a sense of admiration for the zeal and penetration with which it has been conducted, and for the great extension of genetic knowledge to which it has led—greater far than has been made in any one line of work since Mendel's own experiments.

IS VARIATION A REALITY?[1]

[*Nature*, XCIX, 1917]

Dr Lotsy's book is one of many signs that biologists are growing uneasy about the adequacy of evolutionary theory. By whatever doubts the doctrine of Selection was assailed, it has hitherto been common ground that in their generations the forms of life varied abundantly, and that somehow through these variations the diversity of species had come to pass. Modern genetic research has led to the paradoxical discovery that much of the best evidence of variability is capable of other interpretations. Consider the "variation" of any polymorphic moth. No one doubted that from any of the varieties any other might be bred. Now we see that was a mistake. Such variation is not promiscuous, and the varieties are really an orderly series consisting of distinct types which will breed as true as any species, and of mongrel forms which can throw certain fixed types, and those only. The Mendelian conception of the homozygote has raised a new problem. The question arises: Can the offspring of homozygotes vary? Dr Lotsy is sure they cannot. New forms can only come by crossing. That is the thesis of this book. "*Crossing, therefore, is the cause of the origin of new types; heredity perpetuates them; selection is the cause*, not of their origin, as was formerly supposed, *but of their extinction.*"

This is a bold pronouncement, and it contains much of truth. We think not merely of the many species suspected of hybrid origin, but comprehensively of the innumerable species, now perfectly distinct, which can quite reasonably be thought of as segregates derived from some cross ages ago. Few also now believe that the domesticated forms comprising many breeds really had single origins. Apart from difficulties introduced by exact genetic knowledge, modern writers have felt driven to suggest "polyphyletic" origins for pigeons, fowls, dogs, cereals, the common fruits, etc. Almost whenever the history of a modern breed is known it can be traced to a cross. Dr Lotsy took over a wonderful F_2 from a cross in Antirrhinum made by Prof. Baur, and, as he rightly says, it contained many types capable of perpetuation as incontrovertible species. Most geneticists have seen such series and been tempted to similar conjectures. But Dr Lotsy is for taking still wider flights. Geology shows, he says, that new classes

[1] Review of J. P. Lotsy's *Evolution by means of Hybridisation*, The Hague, 1916.

appear suddenly with many highly differentiated forms—the Cycads, for instance, of Mesozoic times. May not they be the direct consequence of some cross? Perhaps; but whence came the original diversity? Why were there distinct forms ready to be crossed? We find no answer to that fundamental question. In the view of the present writer, too, the doctrine of invariability of the homozygote cannot be maintained. Variability is rarer than we supposed, but it is a genuine phenomenon witnessed in unimpeachable examples.

The book will do good if it rouses any reader from the torpor of an easy orthodoxy. It may excite doubts, if it cannot allay them. The language and printing of the book make it something of a curiosity. Cosmopolitanism is a virtue we are glad to meet in these days. Still, English *à la Hollandaise* is a sore distraction in a serious book.

THE DETERMINATION OF SEX[1]

[*Nature*, CVI, 1921]

THOUGH Professor Goldschmidt's treatise on sex-determination is in scope similar to the text-books published by Doncaster and by Morgan in 1912, knowledge has increased so rapidly since then that there is plenty of room for a new statement. Moreover, as the author has himself devoted several years to the study of a special case which departs from the ordinary rules, his views will be of interest to geneticists. Up to a point, the mechanism of sex-determination is clear. On the one hand, we know that in several birds and some Lepidoptera the female is heterozygous in sex, but we have equally sound proof that in man and in several insects other than Lepidoptera the condition is reversed, the female being homozygous and the male heterozygous in respect of the sex-factor. The evidence for these conclusions is mainly either genetical or cytological. With the exception of Drosophila, which, after some doubt, observers have agreed to regard as having the male XY and the female XX, there is no specific form in which positive evidence of both kinds, genetical as well as cytological, can yet be produced. The absence, however, of such convergent testimony need not trouble us at this stage, for each class of proof is by itself adequate so far as it goes. On the whole, also, though difficulties are met with in special examples, the evidence from operative and other collateral observations agrees well with the conclusions deduced from genetical and cytological sources.

Sex being, then, decided by the contribution which one or other of the gametes makes to the offspring, how shall we account for cases in which these seemingly predetermined consequences can by interferences of various kinds be disturbed? Evidence of this description falls into several classes, and its consideration forms a chief purpose of the present book. Hitherto the most famous is that provided by R. Hertwig's experiments on frogs. By delaying fertilisation, he found that the proportion of males could be greatly increased. The suggestion that the females had died off was shown to be inapplicable, and there seemed to be no escape from the conclusion that eggs which in the ordinary course would have become females did after, and presumably because of the delay in fertilisation, become males. The

[1] Review of R. Goldschmidt's *Mechanismus und Physiologie der Geschlechtsbestimmung*, Berlin, 1920.

fact, however, that the maturation-divisions in the case of the frog occur after the eggs are laid offered, as Hertwig pointed out, a possible, if rather unlikely, solution; for the artificial delay might have some influence in deciding which elements should be extruded in the polar bodies, and thus the sex-ratio might be disturbed. Quite recently Seiler, a colleague of Prof. Goldschmidt's, claims to have actually witnessed consequences of this kind following upon the introduction of special conditions in the case of the Psychid moth *Talæporia*, and to have obtained cytological evidence that a rise of temperature during the reduction-division caused the X-chromosome to stay more often inside the egg, and so increased the proportion of males, whereas a lowering of the temperature had the contrary effect. In the case of the frog, even if the delay does act in the way surmised, various difficulties remain to be elucidated, and before definite conclusions can be reached as to sex-determination in Amphibia, and fishes also, we require strict genetical proof as to which sex in those animals is heterozygous in the sex-factor.

Much more serious difficulty arises from a class of fact to which Standfuss was, I believe, the first to introduce us. He found that in Lepidoptera hybridisation might affect the sexes differentially, producing in certain crosses males only, in others predominantly males (the few females being sterile), and similar phenomena proving that the influence of the cross was not alike for the two sexes. A result obtained by an amateur named Brake led Prof. Goldschmidt to investigate a most remarkable case of such differential influence. *Lymantria dispar*, the gipsy moth, is represented by various races all over the northern temperate regions. The sexes are very different, the male being small and dark, the female large and pale in colour. The original observation was that, whereas crosses in the form Japanese ♀ × European ♂ gave in F_1 the two sexes distributed as usual, the reciprocal cross, European ♀ × Japanese ♂, produced normal males, but *females more or less modified in the male direction*. Eggs, therefore, which, if fertilised by the sperm of European males, would have produced females gave rise to "intersexual females," as Prof. Goldschmidt calls them, when the sperm came from these Japanese males. To investigate this curious problem, he proceeded to Japan before the outbreak of the war, and when Japan became involved he went to the United States, where he was interned and encountered other serious difficulties when that nation also joined the Allies. But in the course of his travels he was able to collect and

experiment with a long series of species or local races inhabiting various parts of Europe, Japan, and North America, raising something like 50,000 specimens. Obscure as the meaning of the phenomena still is, there can be no question that when the full interpretation is unravelled the work will be admitted to have an importance at least proportionate to the astonishing labour which has gone to its production.

In outline the main result claimed is that the various races can be arranged in a scale ranging from the "strongest" to the "weakest," and, this series once established, the consequences of mating made between races occupying different positions on the scale can be predicted with considerable accuracy. Intersexual females appeared whenever the male of a "stronger" race was mated with the female of a "weaker." The intersexuality in its several degrees might affect all the sexual characters, primary or secondary, and in its higher manifestations the instincts also. Where such a diversity of features is concerned, a quantitative scale must obviously be largely a matter of individual judgment, but it is claimed that the amount to which these females were modified in the male direction was roughly proportional to the interval between the parent races on the scale of strength; and in the extreme case, when the strongest male was mated with the weakest female, the brood generally consisted of males only, which are interpreted as being in part aboriginal, genetically determined males, and in part individuals which would have been females but for the disturbing influence which has transformed them into males.

Other matings led to the production of intersexual *males*. The discrimination between the two kinds of intersexes was not, to judge from the illustrations, so difficult as one would have expected. The intersexual males appeared with some regularity in F_2 from the cross mentioned above (Japanese ♀ × European ♂) as giving all normals in F_1 and in certain other families besides. There were also some considerable all-female families. Throughout the complicated series of matings glimpses of order appear which suggest that a comprehensive solution is not very far off. It has, nevertheless, not yet been attained. One of the most curious features, as yet inexplicable, is the fact that in the matings giving all-male families females occasionally appear which are perfectly normal, though their sisters are supposed to have been wholly transformed into males.

The interpretation which Prof. Goldschmidt proposes cannot be adequately expressed in a brief statement. He is under the influence

of the theory that each sex contains the potentialities of the other, a conception to which it is now not easy to attach a precise, still less a factorial, meaning. He is disposed to regard the sex ultimately assumed by a given zygote as decided by a struggle or reaction taking place between two components: (1) the sex-factors brought in by X-chromosomes, and (2) a substratum conceived of as inherent probably in the cytoplasm, and capable by its own development of conferring potentialities opposite to those borne by the factors proper. To these opposing elements numerical values are assigned, arbitrarily as it appears to me, and I have been unable to discover in what way the analysis thus offered differs from a restatement of the empirically observed facts, nor is the representation of the all-male and all-female families as alternative end-products of a balanced reaction at all satisfactory. During the period covered by Prof. Goldschmidt's experiments, phenomena closely analogous have been discovered by J. W. H. Harrison in the Bistoninæ. Evidently we are thus brought into touch with a set of facts, probably abundant in nature, which must be accounted for before the problem of sex-determination is disposed of; but, paradoxical as these occurrences are, they do not justify a return to earlier stages of confusion. The problem created by the existence of intersexes, gynandromorphs, and other sex-monstrosities bas always been realised. The case of the free-martin, though its true nature is now settled by the brilliant work of Lillie (well summarised in Prof. Goldschmidt's book), proves that influences as yet little understood may be taking part in these determinations.

An interesting attempt was lately made by Morgan and Bridges to apply the chromosome theory rigorously to a number of mosaic gynandromorphs which have appeared from time to time in the pedigreed work on Drosophila. The parental composition being known, it could be shown from the distribution of the sex-linked factors that in nearly every case these curious patchworks might be represented as resulting from a presumably accidental elimination of a sex-chromosome from the affected parts of the body. The result was certainly a striking one; but this interpretation is not readily applicable to intersexual forms which are not mosaics. Admitting, however, that in mosaics *something* may have been eliminated from the affected patches, the suggestion that this something is the sex-chromosome raises the questions: Why do not the miscellaneous variations, to which the chromosomes of somatic tissues are con-

spicuously liable, more frequently show their consequences as somatic patchworks? and, conversely, Why are the chromosomes of normally dissimilar tissues not themselves dissimilar? But, apart from difficulties to which that line of argument must immediately lead, the occurrence of the intersexes among Prof. Goldschmidt's moths can scarcely be a consequence of accidental elimination, inasmuch as they came with extraordinary regularity. Appeals to the action of "hormones," from which he hopes a good deal, are a mere veiling of the difficulty. No one will dispute that these products are part of the proximate mechanism by which the effects of sexual differentiation are produced; but the problem of sex-determination is to discover the influence which primarily causes that differentiation to proceed in one direction rather than in the other; and herein, where the evidence of gametic differentiation is insufficient, we are left without any plausible conjecture. In considering the characteristics of partly or wholly sterile forms, it may be worth remembering that in proportion as a zygote is sterile, it *may* be retaining elements which, if it were fertile, would be extruded in its gametes. May not this retention influence the characters of the zygote?

Like its predecessors, this book expressly abstains from the attempt to deal with the problem of sex-determination in plants. We cannot quarrel with the wisdom of that decision, for the truth is that we are very far from any workable scheme which can be applied to them; but it is unfortunate that the diagram put forward by Correns as a representation of his views on sex in Bryonia should be chosen as the model of a "digametic" system of sex-determination. The author does imply that he has misgivings about that illustration, which, as I have elsewhere shown, is quite inconclusive. The incautious reader could scarcely avoid the inference that the scheme of sex-determination applied to animals is one which had been proved to hold in the case of a flowering plant—a very misleading conclusion.

Another region of the subject still altogether obscure is the genetical relation of the unisexual to the functionally hermaphrodite forms in animals. Prof. Goldschmidt's book contains all that can yet be said on that difficult question. There are, of course, various sorts of monœcism, and for scarcely any of them have we yet even an acceptable cytological scheme, still less any genetical evidence.

The book, as a whole, is very well done, and may be recommended to all students who wish to have the latest presentation of the facts in a clear and readable form. As I have implied, there is a want of

lucidity in the discussion of the problem of the intersexes, and trouble would be saved to the reader if he were at once told that he will not be presented with a real solution. If he reads the book carefully he will discover that for himself; but the series of facts is exceptionally interesting and, at the present stage of genetical theory, of such vital importance that the effort will not be wasted.

AREA OF DISTRIBUTION AS A MEASURE OF EVOLUTIONARY AGE[1]

[*Nature*, CXI, 1923]

To determine the value of Dr Willis's book is not easy. The author delivers his message with enthusiasm and emphasis. "Age and Area," he reiterates, provides a penetrating and wholly new light on evolution. His supporters, four of whom contribute chapters to the book, endorse this opinion and tell us it is all right. Table after table exhibits special phenomena on which Dr Willis relies. These tabulations seem to have been scrupulously made, and they certainly demonstrate some remarkable and novel results. The book is written with perfect sincerity and a conviction almost naïve. Whatever its worth may prove to be, it is an honest attempt. So imposing an array must produce an effect in the mind even of the critical. But there are disquieting features. Repetition of the bald assurance that Age and Area is the true faith should be unnecessary. A judicious advocate would leave that conclusion to flow more quietly from the evidence. When, for example, we read, "As one of our leading ecologists says in a letter to me, and underlines, 'this will be strongly in favour of your Age and Area hypothesis,'" we remember seeing testimonials like that elsewhere and in more mundane application. But though the reader's scepticism is thus instantly aroused, the matter is worth careful attention, for to have hit on a new method of investigating even a part of the theory of evolution is no common achievement, and that the author has done this cannot in fairness be denied.

The main idea is not difficult to grasp. It is simply that, subject to various provisos, the area which a species "occupies" upon the earth is a measure of its antiquity in evolution. "Occupy" is scarcely a fortunate word in so formal a definition. The area "occupied" by a species has immediately to be explained as meaning the area over which the species *extends*, or has extended as shown by the fossils. Lingula lives now in the Chesapeake and in Philippine waters, but to speak of it as "occupying" the whole world would be confusing, even though it is found fossil in many countries.

A species once evolved is conceived as spreading in an ever-widening circle, much as a culture may do, inoculated upon a gelatine plate. If the medium be homogeneous and growth be undisturbed,

[1] Review of J. C. Willis's *Age and Area*, Cambridge, 1922.

the size of the circle will be a function of the age of the culture until the medium is covered. The species or genera in the course of their dispersal are held to throw off new species and new genera, each of which again spreads concentrically from the focus of its inception. The throwing off of these new forms of life is regarded by Dr Willis as a "casual" process, and regarding it some very definite inferences are drawn, of which we will speak later.

Now every evolutionist agrees that, *apart from disturbing elements*, area is a measure of age. If the matter rested there nothing would be in dispute, but nothing fresh would have been contributed to the discussion. We are, however, asked to believe that in practice this mode of estimating the age of a species is, on the whole, trustworthy: that endemic species and rarities in general can and must be for the most part accepted as new starters in evolution, and not as survivors. That is, of course, a paradox, but it constitutes the main thesis of the work. Dr Willis takes the floras of Ceylon and New Zealand into special consideration, besides those of other isolated places, mountain tops and remote islands, and in brave defiance of all that science has hitherto taught us regarding the peculiar plants and animals limited to such localities, he tells us that, on the whole, the reason why those creatures occupy such small areas is that they have not yet existed long enough to have spread far. If anyone objects that in application to the special cases which immediately suggest themselves, Sphenodon, the dodo, Leucodendron, etc., such a contention is preposterous, Dr Willis would reply that he knew as much already, and that he is concerned not with special cases, but with averages and general propositions. He is within his right. The second proviso is that comparative estimates of age are only to be based on area when forms within the same "circle of affinity" are compared.

Everything then turns on the computation of these averages and on the criteria by which "circles of affinity" are to be recognised. Unfortunately no means are suggested by which we are to tell whether a species or genus is a novelty or a relic, and obviously none can be forthcoming. We may make shrewd surmises, but if things like that could be declared with certainty the study of evolution would be on the way to becoming an exact science. Meanwhile estimates of age based on area "occupied" must be exceedingly hazy. Giant tortoises live in the Mascarenes and in the Galapagos, and therefore must be reckoned ancient, as they doubtless are. When they become extinct, say in the Mascarenes, which they presumably will, they would start

again as novelties at the bottom of the list, but for the accident that the remains of such creatures form conspicuous fossils. Of the New Zealand shrubby Veronicas one, *V. elliptica*, occurs also in Fuegia; having the widest recorded range it must be deemed by far the oldest of these species. Once extinct in either locality, whether Fuegia or New Zealand, it would be ranked with the rest of the New Zealand species as new mutations.

Then again the surface of the terrestrial globe is, as we all know, a medium of complex heterogeneity. By no provisos, safeguarding clauses, or anticipatory exclusion can considerable areas be defined in which dispersal may be observed which has not been promoted or limited, diverted or arrested, by countless interferences. Very rarely, if ever, do we find that reasonable uniformity and constancy of conditions, even in space, let alone time, without which we are warned the theory must not be applied. In areas which may be judged most uniform at a given point of time, tbe operation of sharply limiting causes is manifest. If, as in prairies and steppes, for hundreds of miles the conditions appear geologically and meteorologically uniform, the mere presence of living things introduces heterogeneity. Dr Willis is well aware of this. In one of his best chapters he discusses "barriers" in the widest sense, and he makes us realise how difficult it must be for a new-comer species to get a footing or to spread among plant-associations already established. On the Central Asian steppes, for example, one can distinguish on the remote horizon by their colour the spots where encampments have stood. These patches are mainly characterised by the presence of nettles, which grow in such places. Nettles, as Dr Willis remarks, are very easily dispersed by wind, yet nowhere else do they establish themselves in the Artemisia steppes—only in places which man and his animals have made fit for their growth. European weeds abound in the Eastern States where the soil has been cultivated, but few invade patches of unbroken territory. Quantitative estimates of the allowances to be made for heterogeneities and barriers in general cannot be attempted. Therefore in the hope that the heterogeneities will be so many and so various as to cancel, a reservation is introduced to the effect that the groups of species to be compared should each be not less than ten in number. But the difficulty is a real one, and in dealing with any troublesome or unconformable phenomena these considerations provide endless loopholes for escape.

A still more formidable difficulty is encountered in the endeavour to

declare which classes of forms may be compared legitimately with the object of determining their relative ages from the areas they occupy, and which are not comparable. To have some consistent criterion by which comparables may be recognised is absolutely essential to the application of the method. Nevertheless no information offered reduces the difficulty materially. We are told that only forms in the same "circle of affinity" are to be taken—a definition which is plainly left vague deliberately. How this is to be construed we are never precisely told. The species to be compared must be more or less alike in their modes or at least in their facilities of dispersal—a property we have commonly no means of estimating in any trustworthy or quantitative way. Unless I have misunderstood the chain of reasoning, its validity is severely strained at this point.

The author is shy of special illustrative examples and they need not be essential to an argument dealing solely with general propositions, but in a chapter contributed by Prof. Small we are provided with an illustration on the largest scale. There we are given to understand that the natural order Compositæ is a "circle of affinity" to which the method of Age and Area can be properly applied. If a group so polymorphic and heterogeneous as the Compositæ constitute a "circle of affinity," the members of which can be compared for these purposes, where are we to stop? The tribes of Compositæ are arranged in a genealogical tree upon which the presumed point of origin of each is marked, and we are told that the order of evolution as given on the tree, which has been constructed from anatomical data, agrees substantially with the numerical estimate of the areas occupied by each tribe. Needless to say, numerous eminent botanists have arranged the tribes in almost as many other ways, probably with equal propriety. These speculative genealogical trees, once fashionable, are, I had supposed, discredited. All that they can attempt is the display of a logical order of interrelationship based on the modifications of the special set of organs selected as a criterion; for the Compositæ this order will differ with each set of organs chosen. In support of Prof. Small's arrangement he gives an imposing tabulation of the geological levels in which each tribe is believed to have arisen. Not until the text of Prof. Small's previous papers is consulted does a reader discover that this tabulation is almost wholly conjectural. In a well-written and judicious chapter by Mrs Reid, who discusses what palæobotany can produce in support of Age and Area, we find no such confident pronouncements. The inclusion of the chapter on the Com-

posites reflects more credit on Dr Willis's candour than on his scientific judgment. The propositions made in the name of the theory there stand forth with a neglect of caution which Dr Willis himself seldom exhibits.

For the reason given, the theory of Age and Area, except in so far as it is truistical, is as yet of doubtful value, and unless amended to meet the difficulties specified it cannot be applied with any confidence. I suspect that certain predictions respecting the flora of the islands near New Zealand, which, though made in advance, as we are frequently reminded, were fulfilled, did not involve any feat of which common sense would have been incapable.

Dr Willis is a great advocate of the theory of mutation in its crudest form. The speculation now presented to us as Age and Area is a development of an idea which came to him when he reflected on the fact that in Ceylon several endemic species are limited to small areas, though sometimes associated with related species of wider distribution. The theory of mutation of de Vries appeared at about the same time, and Dr Willis asked himself whether the wonderful "mutations" which had been reported in Œnothera might not exemplify the process by which the Ceylonese endemics had been begotten by the "wides," as he calls them. Endemics had previously been held to be largely relics. In the new light they become "in the vast majority" novelties, about to spread with the lapse of time in widening circles. On any theory of evolution endemics must be in part novelties and in part relics; but why, apart from the theory of Age and Area, we should believe that endemics are in such great majority novelties I do not clearly understand, for though we know little of origins we are certain that myriads of species have become extinct. It is surely contrary to all expectation that the process of extinction should be in general so rapid, and the final endemic phase so short that the number of species in that final stage of existence should be insignificant.

The supposition implies the optimistic but embarrassing corollary that a species, once established, is in no great danger of extermination unless some catastrophic or lethal change occur in the conditions of life. *Cupressus macrocarpa* is admitted to be in danger because, as we are told, the Monterey peninsula is drying up. This is used as the stock illustration of the mode in which authentic extinction should occur. As it serves three times in this capacity, bearing perhaps an undue burden in the argument, we may infer that examples of extinction through predicable secular change are not plentiful. Unless, indeed,

the change can be traced directly or indirectly to human action, the cause whether of gain or loss of territory is apt to be a mere matter of surmise, for though losses are so familiar we must not forget that there are also mysterious gains—even in our own area. Who shall say what gave *Capros aper* its chance? A doubtful British species in the time of Couch, it became a nuisance in the trawl, some time at least in the eighteen-eighties. How did the showy *Plusia moneta* become a common British moth? No one recorded it here before 1890. Extinction must ensue from countless causes. If compelled to specify one class of cause as operating rather than another, we should regard the appearance of a new and antagonistic organism as by far the most formidable and effective agency of extinction; but we have only to glance at anthropological data to observe that no rule obtains as to the length of time which the process of extermination will take. Whatever doubts be entertained as to the significance of adaptation in delimiting *specific characters*, there can be none that survival is determined by selection according to the balance of the profit-and-loss account on the workings of the machine.

Wondering at the Ceylonese endemics, Dr Willis asks rhetorically, "Had one arrived in Ceylon just in time to see the disappearance of a considerable flora?" We may reply, What more likely? Is the alternative interpretation, that he had come in time to attend the birth of a new flora, more acceptable? About half the endemics of Ceylon, he tells us, occur on the tops of single mountains or small groups of mountains. Does he really suppose that future ages will witness the spread of such species downwards from the mountain tops?

In reading the chapter on the origin of species and the many passages in which references to mutation are made, I see signs that Dr Willis, though making large assumptions in the name of genetical experiment, is not sufficiently conversant with the present state of genetical science. Both from observation and from experiment, the certainty that variation is largely discontinuous has been established. If for the moment we abrogate the consideration of interspecific sterility we might declare that forms mistakably like new species do actually arise suddenly. But this is scarcely mutation as contemplated by the theory of Age and Area. If we were told categorically which "wide" species is regarded as the putative parent of which endemic, we should be in a position to consider how far this interpretation is consistent with what we know of variation. From anything so precise Dr Willis shrinks. Here and there we get a glimpse of what he would

like us to infer. The endemic *Coleus elongatus*, for example, he is inclined to claim as the immediate product of *C. barbatus*, from which it differs in some ten respects. The shrubby Veronicas are characteristic of New Zealand; if pressed Dr Willis would point to the "wide" *V. elliptica* (mentioned above) as their putative parent. Similarly the Chilian *Ranunculus acaulis*, or alternatively *R. crassipes* (found in Kerguelen), which both occur in New Zealand, might be adduced as the parent of the endemic Ranunculi of those islands. Though undeniable as possibilities, we have to consider what warrant for such guesses can be drawn from the observed facts of variation. The answer is quite clear that up to the present scarcely anything comparable has been observed. The "rogue"-peas, the "fatuoid" mutations of oats (Nilsson-Ehle and later Marquand), with perhaps a very few more, are all that can be quoted as precedents, none certainly in point. No one familiar with genetical work would be disinclined to entertain the supposition that such groups of endemics as the New Zealand Veronicas may not improbably be co-derivatives from one or more crosses; so also may the hosts of "species" of Cratægus which Prof. Sargent has described largely as endemics on derelict farms of the Eastern States. But to establish these propositions, genetical and doubtless cytological work on a vast scale is required, and far too little has been yet done to justify the bold assumptions lightly made in the doctrine of Age and Area.

The evidence adduced by de Vries from Œnothera which led him to propound the theory of Mutation is clearly enough the precedent which Dr Willis has at the back of his mind. From the first the meaning of the Œnothera work was ambiguous. The researches of Renner and of Heribert-Nilsson have now shown that those early suspicions were justified, and that the "mutations" of Œnothera are not genuine illustrations of the origin of species by variation in descent from a pure form. Had de Vries grasped the implications of Mendelian analysis, he could never have so interpreted them with any confidence. The few words in which he conveys his benediction on this new venture should be read with caution and reserve by persons unfamiliar with the history they purport to relate.

Unconvincing as the main argument of "Age and Area" appears, the reader will find in it some curious and interesting discoveries. Of these the most remarkable is the uniformity of the statistical distribution of species among the genera of various and most dissimilar forms of life, both plants and animals. The monotypic genera,

with one species each, are always the most numerous, commonly forming about a third of the whole group, the ditypics, with two species each, are the next in frequency, genera with higher numbers of species becoming successively fewer. Set out graphically, according to the number of species they contain, the genera exhibit what is here called a "hollow curve" of frequency, and there is no gainsaying the fact that these curves, though collected from such miscellaneous sources, have a remarkable similarity. Another curious feature exhibited by this marshalling of the genera according to the number of their species is not merely that the percentage of monotypes is largest on islands (as might be expected), but that it is exceptionally high in South America and in Africa. The corresponding curves from several other regions are altogether different. I do not wholly follow the argument by which these features of regularity are interpreted as giving strong support for the theory of Age and Area. Whatever be the meaning of the regularity of the curve of frequency of species distributed according to genera, the occurrence of order in this unexpected place does not readily accord with the Darwinian view that specific diversity is primarily or closely dependent on fitness. That deduction, which looked so attractive in the superficial survey which was all that could be undertaken in Darwin's time, became practically untenable so soon as the phenomena of variation were accurately explored, and it is not surprising that close investigation of another part of the species-problem has revealed a similar weakness.

On the other hand, though the point is a minor one, the considerations collected under the title "Size and Space," though adduced as fatal to the theory of Natural Selection, seem to have little cogency. On the average, genera with more species are shown to extend over greater space, and hence the area occupied by a genus corresponds roughly with the number of species it contains. What else could we expect? A large college, with a larger and more varied supply of competitors, commonly shows more success (and indeed more failures) in more varied departments of activity than will be achieved by a smaller establishment.

One excellent purpose Dr Willis's book will certainly serve. It will renew the debate on the mode of evolution, which for many reasons has of late years languished. Whatever doubts arise regarding the new deductions, Dr Willis once more makes geographical distribution a live study, showing quite unexpected lines along which it may be pursued. The delimitation of floral areas—or, for that matter,

zoological areas too—was, as he says, a dull and almost futile exercise of scholasticism. The introduction of statistical methods, here altogether appropriate, offers great possibilities.

In stronger hands a still greater effect might have been produced. The style of presentation scarcely attains the level required of such works by an age not over-exacting in that respect. Finish is no longer demanded of scientific authors, and we have come to suppose that loose writing is compatible with clear thinking. None the less it makes very difficult reading. Those who are not alienated by such blemishes will find the book interesting as a challenge. How far the new ideas are of value and how many of them are fallacious we shall scarcely know till they have been tried in practice over wide fields of experience, and examined in perspective from many aspects.

MENDELIANA[1]

[*Nature*, CXV, 1925]

(1) In honour of Professor Correns's sixtieth birthday, the German Society for the Study of Heredity has reprinted most of his papers relating to genetical subjects. They compose a very substantial volume of 1300 pages. The subjects of this prolific labour have been numerous, but after his large work on cross-breeding the varieties of Maize, Correns has mainly been occupied with two of the most intricate problems of botanical genetics, the transmission of variegation and the determination of sex in plants. Regarding the first of these phenomena, owing to the vast diversity in the physiological nature of the several kinds of chlorophyll defect, general expressions are obviously unattainable. Variation, in fact, is a symptom. Everything depends on diagnosis, which though sometimes easy is commonly difficult and evasive. Through contemporary work, especially that of Correns, those who come after will at least find the facts set out ready to be disentangled.

The problem of sex-determination in plants is still more complex, and no simple and generally acceptable solution is yet in sight. The tendency of modern opinions is in favour of the view which Correns himself has advocated, that in diœcious plants the male is the heterogametic sex, but this interpretation is not wholly free from objection. In plants, as also to some extent in animals, an outstanding difficulty is the complete absence of any satisfactory account of the relationship of the hermaphrodites to the sexual forms. Correns was the first to observe the remarkable fact that in gynodiœcious plants the offspring of females are generally in a large majority females, those of the hermaphrodites consisting predominantly, sometimes entirely, of hermaphrodites. This is now recognised as being only a special case of a system of inheritance governing that of a great variety of characters. The essential phenomenon is genetical inequality between the eggs and pollen grains of the same plant, of which many examples are now familiar, the inheritance of double flowers in the Stock being the original and classical illustration. The simplest interpretation, to which many of us in England have inclined, is that a segregation,

[1] Reviews of C. Correns's *Gesammelte Abhandlungen zur Vererbungswissenschaft aus periodischen Schriften*, 1899–1924, Berlin, 1924, and of H. Iltis's *Gregor Johann Mendel, Leben, Werk und Wirkung*, Berlin, 1924.

probably somatic, has occurred prior at least to maturation, but those who, like Correns, are unwilling to admit anything which conflicts with the strict chromosome-theory, seek for some other account. Much ingenuity has been devoted to an attempt to demonstrate the existence of the missing class of pollen grains, and the numerous papers dealing with this vexed question form a prominent feature of the present volume. Even if it were proved that pollen grains of the missing classes—always recessive by the way—are produced by the plant in the normal proportion, the peculiarity in their behaviour would remain to be accounted for.

Correns was, of course, one of the rediscoverers of Mendel, in a sense, perhaps, *the* rediscoverer. The earliest papers in this volume recall that curious and diverting episode, and the cryptic nature of the first announcements. In view of all that has happened since, he may, in any case, find satisfaction in remembering that in 1902, some time before linkage had been observed as an actual fact, he made a suggestion (p. 304 in this collection) as to the linear arrangement of elements in chromosomes and as to the exchanges between them, now spoken of as crossing-over, which in all essentials is that now adopted by the orthodoxy of the day.

The frontispiece reproduces a portrait-drawing of the author by Hans Meid, which is a very brilliant performance, both as an exact and penetrating portrait and as a piece of artistic workmanship. In spite of its high price many libraries should get this book, for several of the papers here assembled from various journals will be in requisition for some years to come.

(2) Contrasted with the imposing length of Professor Correns's output, the slender memoir which, by the piety of Dr Iltis, of Brünn, tells us all we are ever likely to know of Mendel himself, makes a modest appearance. The story of his life is in outline familiar. Any details about such a man are welcome, and the few new facts and anecdotes now first made known help us in some measure to reconstruct his personality, but the generation that knew him during the years of his scientific work had almost passed away before his fame began, and as to many essentials we have nothing but surmise.

It is the old story of the boy of sturdy peasant family noticed by an intelligent teacher and selected for education and promotion. We learn that in his village school some natural history was taught at the instance of the great lady of the place, an advantage which no Gymnasium would have supplied. The children even saw something

of fruit-growing and bee-keeping in a garden attached to the school, so much so that an inspector, reporting on the school to the Archbishop's Consistory, complained of this disorder (*Wachsthum dieses Unfugs*), which he said was chiefly due to the machinations of a certain Pfarrer Schreiber. That gentleman had done much to promote fruit culture in the district, and as it is also known that Mendel's father took special interest in fruit-growing, we may take it that nature and nurture seem thus to have combined happily for once. Regarding the later stages of his education, details are tolerably full. As a curiosity may be mentioned two fragments of an academic poem in praise of Gutenberg, which, though rather wooden and rough, is not without imagination. It was written when Mendel was seventeen or eighteen, and is interesting as containing the following lines, addressed to the movable types:

> Ihr sollet nach des Meisters Wunsche
> Des Aberglaubens finistre Macht,
> Die lastend sich auf Erden wälzt,
> Zerstreun;

an ominous beginning for a future Prälat, as Dr Iltis observes.

The funds for his further education were provided by a sort of mortgage of the small paternal property to Mendel's brother-in-law—a remarkable document which survives. It gives a full inventory—two horses, four cows, one heifer-calf, one bull-calf, etc.—so that a clear picture of the family circumstances is before us. Being destined for orders and the teaching profession, he was sent for his continued education in "Philosophy" to an establishment of Olmütz, where his health seriously broke down more than once. Financial difficulties also supervened, and, as Dr Iltis says, it hung by a hair whether there should be one peasant the more and one immortal discoverer the less in the world. Money was found by the devotion of a sister, then unmarried (whose three sons afterwards became Mendel's especial charge). But the strain to health lasted, and Mendel, when his course of "philosophy" was at length over with distinction, felt unequal to renewing such an effort and consulted a certain Professor Franz as to his future. Franz had some influence with the Brünn cloister, and, having great confidence in Mendel's character and abilities, got him admitted to the brotherhood.

The chief authority for this part of Mendel's career is a brief autobiography which he prepared later on (*æt.* 28) when he was a candidate for a permanent post as a teacher in the Znaim Gymnasium. He had

already a post as assistant in this Gymnasium, but in order to become permanently appointed, he required a certificate of official recognition. The procedure on this occasion (1850) strikes us as singular. He had first to supply a full and intimate history of his career, and mental development, etc., together with an inquisitory report on his behaviour from the teaching staff of Znaim. They speak well of him, the only charge they have against him being that he had been six times to the theatre, admittedly a venial error since on each occasion he had gone in the company of a colleague. The next step was the preparation of what must have been almost small treatises, one on meteorology, the other on a geological subject, for which six or eight weeks was allowed. These were referred to experts, and, in addition, to a literary assessor, who all reported upon them at elaborate and pedantic length. Ultimately, on the unfavourable verdict of the geologist, he was rejected. The papers with the reports have been preserved. We get the impression that if the business of academic education was always conducted on those lines, he was well out of it. He would have had little time for peas. So he returned to the Brünn fraternity, teaching without a qualification. The failure anyhow had one very good consequence, for it led indirectly to his being sent to the University of Vienna for two years, apparently with a subsidy from his cloister. In 1856 he made a second attempt to obtain the official qualification necessary for the teaching profession (p. 59), offering then physics and natural history. The result is not clearly recorded, but he was evidently rejected, for until he became Prälat he always figures as "Supplent," not lecturer or professor like his colleagues. None the less his fame as a very successful teacher still survives in Brünn, and these incidents provide ironical commentary on the public utility of a highly regulated educational system.

Mendel's pupils contribute the interesting reminiscence that at some early date one of his two rooms at the cloister was given up to birds and to mouse-breeding, and his biographer conjectures that possibly dominance and segregation were first seen in the mice. Dr Iltis points out that some experiments with peas must have been already in progress in 1854, for in that year Mendel published an observation on *Bruchus pisi*, which had been damaging peas near Brünn. His interest in the species problem was probably aroused by Gärtner's experiments, though that must be uncertain. How the work fell unnoticed we all know. In spite of an exchange list of 120 copies which went to the various libraries and 40 private *separata*,

not one soul took any heed of it. He remained alone. After his immense labour he found not a single creature who understood, not one who believed him. As bad luck would have it, he then started on Hieracium, and then in an evil moment he tried to interest Nägeli, whereupon ensued that tragic correspondence which completed the catastrophe. Nägeli understood him no better than the citizens of Brünn, and, after waiting two months, replied from Olympian heights that the pea experiments seemed to have only just begun, and that he had better go on with Hieracium. The later letters all relate to Hieracium. Nothing more is said about the peas. Nägeli is known to have sown the peas which Mendel sent him, but there is never a word as to how they behaved. Hieracium must have been a crushing disappointment, for apogamy was not discovered until long after. That was not Nägeli's fault; but perhaps we may draw the moral that a discoverer of something really new, wishing to find sympathy and encouragement, does not act wisely in appealing to the highest established authority on that particular subject. Dr Iltis pessimistically remarks that his remedy would have been to have published it all in a "stattliches Buch," as no modern investigator would have neglected to do—something more like Correns's, in fact. This course, nevertheless, has also been known to fail.

All attempts to find the records of Mendel's experiments on bees have failed. We have only the plan of his hives, preserved by the carpenter. He worked on many other subjects, notably Fuchsia, but of these investigations also the results are lost.

We have next a full account of Mendel's meteorological observations, and the life concludes with a detailed history of his "fight for right" against the vindictive taxation of religious houses which was instituted by the Austrian Government in 1874, another painful story. At first he was backed up by the heads of other convents and by the brethren in his own, but after a while they all abandoned the struggle. Once again, in this last enterprise, he was utterly deserted and alone. His obstinacy was such that doubts of his sanity were professed. Whether he was right or wrong it is hard to say, but at least he bore himself throughout as a brave and resolute man should.

The second half of the book gives an account of Mendelian doctrine and its later developments up to the present time. This is very well done, and it supplies in a compact form as good an epitome of the modern science of heredity as has yet appeared.

Dr Iltis is convinced that Mendel was virtually a freethinker, and

only officially a Catholic, interpreting various details in this sense. That he had no special call to clerical work is clear. In his early days this was commented on by a superior who, reporting to the Bishop that he led a modest, religious life, combined with much zeal for the sciences, adds that he had little aptitude for the care of souls. Ministration to the sick and dying distressed him so much as to induce serious illness, presumed to have been a sort of hypochondria. Without much stronger evidence I should hesitate to accept Dr Iltis's judgment, which is tantamount to a charge of active insincerity. Rather I should suppose that Mendel's position has that of numberless honest men in all ages the world over, who can take things as they find them. Nothing at all suggests that considerations of faith or douht had much interest for him, or that he was ever in the position of having to take a side on such questions. Probably they never troubled him one way or the other. I imagine Mendel as a man full of practical good sense, with an exceedingly clear head, thinking in well-divided compartments, rarely disturbed by the eccentricities of genius. We are told that he was not given to brooding or to sentimentality, that he was devoid of music and cared nothing for "Belles Lettres." But when roused he showed, nevertheless, that he had in him a strong element of the martyr, as appears very plainly from the protracted resistance to authority which embittered the last ten years of his life; and *primâ facie* such a man is scarcely one whom we need suppose consciously guilty of long-continued sophistry or dishonourable compromise. With this reservation we may be grateful to Dr Iltis for a masterly book, in which all too scanty materials have been used to the greatest advantage, and not least for having rescued one most excellent photograph (p. 53), from which we can at last see exactly how Mendel looked at about the time of his discovery.

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